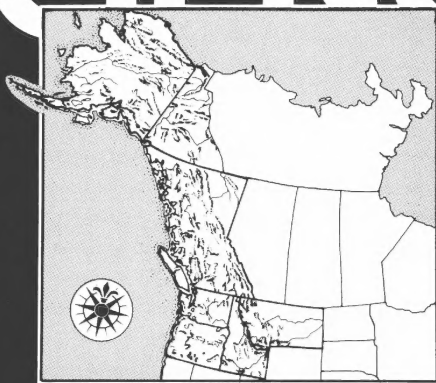


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NORTHWEST SCIENCE



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Once again I express for *Northwest Science* and the Association our special thanks to Caroline Hooper for preparation of the index to volume 62.

Announcements

Annual Spring Meeting

The annual meeting of the Northwest Scientific Association will be held at the Tri-Cities University Center in Richland, Washington, March 21-24. By now you should have received advance registration information and a call for papers. Abstracts will be published in a special issue of *Northwest Science*. A follow-up mailing with further details should reach you around the same time as the February issue of the journal. The Association is again waiving the registration fee for students who present a paper at the meeting.

The Association will also announce at the meeting winners of the student research grants. Besides symposia and contributed papers, several field trips are planned. The Tri-Cities is in the middle of one of the best wine growing regions in the country and the Columbia Basin usually enjoys an early spring. We are looking forward to the meetings and hope you plan to attend.

IN MEMORIAM

GEORGE R. FAHNESTOCK

Friends will be saddened to learn that George R. Fahnestock died in Seattle December 20, 1988 at the age of 74. George graduated in botany from the University of Cincinnati in 1936, received a Master of Forestry degree from Yale University 1938, and a Ph.D. from the University of Washington in 1975.

George had a varied and interesting career in the US Forest Service with service in both National Forest Administration and Forest Research. He held positions as technician in silvicultural research, foreman in a CCC camp, ranger, and fire research specialist. In 1965, he transferred to the Pacific Northwest Station and was Leader of the Fuels Appraisal Project (Seattle) until his retirement from the Forest Service in 1973.

But retirement was only another step in his career. He took on a fire ecology study in the Pasayten Wilderness as his Ph.D. dissertation. In 1978 and 1979 he served as a fire specialist in Alberta with the Canadian Forest Service. George was also an Affiliate Professor of Forestry at the University of Washington. He was a perceptive researcher, an excellent writer, and authored a number of publications, especially on fuels as related to fire control. At the time of his death, he was Secretary of the Northwest Scientific Association.

We will miss his awareness and interest, his keen mind, his wit and boundless humor, and his interest in young people. His death is a loss to his family, friends, and to the forestry profession.

—*Friends and Associates*

and

Elwood G. Bizeau, Wildlife Research Institute, P.O. Box 3246, University Station, Moscow, Idaho 83843

An Estimate of Bias in Tail-Fan Surveys of Rocky Mountain Canada Geese

Abstract

Tail fans from Canada geese (*Branta canadensis*) shot by hunters are examined annually to estimate age ratios (immature/adult). Some immatures completely replace immature (notched) tail feathers with adult (unnotched) feathers before the end of hunting season. To analyze the significance of this molt, two fall estimates of the numbers of immatures and adults in the Rocky Mountain Canada goose population (RMP) were used to calculate expected tail-fan age ratios. The accuracy of these ratios was assessed by estimating the percentage of immatures completing the tail molt to adjust the numbers of immatures (birds with at least one notched tail feather) and apparent adults (adults plus immatures with adult-looking tail feathers) available for sampling in tail-fan surveys. Comparison of the estimated observed ratios to a mean age ratio from the survey indicated reasonable results. Expected tail-fan age ratios were from 0.9 to 1.1 versus an observed ratio of 0.2. Tail-fan ratios across North America were examined in relation to latitude of nesting and suggested that nesting phenology, as it influences the time of molt, is a critical factor affecting the degree of bias in Canada goose tail-fan surveys.

Introduction

Hunters annually submit to the U.S. Fish and Wildlife Service (FWS) tail fans from Canada geese they have shot. These tail fans are examined and used to estimate fall age ratios despite the fact that these ratios could be biased (Sorensen *et al.* 1987). Because some immatures (IM) completely replace the diagnostic notched tail feathers before or during the hunting season, they are misclassified as adults (AD) (Tacha *et al.* 1987), thus causing observed IM/AD ratios to be low. The extent to which tail-fan estimates are below actual fall age ratios has not been determined for most Canada goose populations.

Tacha *et al.* (1987) found that in a sample of known-age Canada geese collected in November and December, 92 percent ($n = 39$) of the immature *B. c. interior* had one or more notched tail feathers compared to only 23 percent ($n = 30$) of the immature *B. c. maxima*. *B. c. maxima* nests in central North America, whereas *B. c. interior* nests in the Hudson Bay region of central Canada (Hine and Schoenfeld 1968:6). Tacha *et al.* (1987) noted that *B. c. interior* nests and molts about a month later than *B. c. maxima* (based on Hanson 1965:118) and suggested that the degree of bias in harvest age ratios is a function of subspecies. We provide evidence that the IM/AD ratios of RMP geese, a mid-latitude nester

(Krohn and Bizeau 1980), were also biased low and estimate the magnitude of this bias. In addition, we examine the effect of latitude on tail-fan age ratios and suggest that the time of nesting and hatching (and hence molting) is a more critical factor than subspecies *per se* affecting the degree of bias in tail-fan surveys.

Methods

The number of Canada geese tail fans submitted from the U.S.A. portion of the RMP's range (see Krohn and Bizeau 1980:6-7,58) and classified as immatures and adults, 1965-1974, was obtained from the FWS's Office of Migratory Bird Management, Laurel, Maryland. These years were selected because they represented a period when the size of the RMP was relatively stable (Krohn and Bizeau 1988) and were within the period covered by population simulations done by Krohn and Bizeau (1980).

Krohn and Bizeau (1980:48-49) examined the population dynamics of the RMP with two deterministic models built with data mostly from the mid-1960's to early 1970's. These models provide two estimates of the numbers of immatures and adults in the fall population. Immatures were 1.29 times more likely to be shot than adults (Krohn and Bizeau 1980:36), and thus the number of adults available for harvest, and hence sampling

in the tail-fan survey, was reduced by 0.78 ($=1.00/1.29$). Because both population models were of unknown reliability (Krohn and Bizeau 1980), the two expected age ratio estimates from the models were checked by assuming a level of bias in the number of immatures misclassified as adults and recalculating observed tail-fan age ratios. This check allowed us to determine whether or not the expected age ratios (from population data) approximated the observed ratios (from tail-fan data). Tacha *et al.* (1987) found that 23 percent of the immature *B. c. maxima* had one or more notched tail feathers, so we assumed that 77 percent of immature RMP geese (*B. c. hoffitti*; Krohn and Bizeau 1980:48) also completed the tail molt before or during the hunting season. Seventy-seven percent is probably a high estimate because it was based on birds examined in November and December (Tacha *et al.* 1987) and a substantial part of the RMP harvest occurs earlier (Krohn and Bizeau 1980:77-93) when fewer immatures have completed the tail molt.

To examine the effect of latitude on tail-fan age ratios, we estimated the number of wintering Canada geese in each flyway coming from northern ($>52^{\circ}\text{N}$. Lat.) and southern ($<52^{\circ}\text{N}$. Lat.) breeding areas. We expected those flyways with a high percentage of northern birds, and presumably later hatching and molting, to have higher tail-fan age ratios. Populations were assigned to flyways, and breeding ranges to north or south categories, by locations as illustrated in Hine and Schoenfeld (1968) and modified for *B. c. hoffitti* by Krohn and Bizeau (1980:45-47). Wintering numbers, 1984-1985, came from the North American Waterfowl Management Plan (Canadian Wildlife Service and FWS, 1986:7) and mean tail-fan age ratios, 1982-1986, were calculated from Sorensen *et al.* (1987:34-35).

Results

More tail fans were classified as adults than as immatures, 1965-1974, with IM/AD ratios ranging from 0.10 (1974) to 0.37 (1969) (Table 1). Linear regression analysis indicated no temporal trend ($F = 1.46$, $P = 0.26$), thus the mean of 0.19 was judged the best tail-fan estimate of RMP fall age ratios.

In contrast, the two population models suggested fall age ratios in the range of 0.67 to 0.83 (Table 2). Considering that adults are less

TABLE 1. Fall age-ratios for the Rocky Mountain Canada Goose Population as indicated by tail-fan surveys, 1965-1974.*

Year	Number of:		IM:AD
	Immatures (IM)	Adults (AD)	
1965	79	292	0.27
1966	57	468	0.12
1967	75	337	0.22
1968	67	371	0.18
1969	82	221	0.37
1970	31	249	0.12
1971	55	258	0.21
1972	45	229	0.20
1973	36	301	0.12
1974	36	359	0.10
$\bar{X}$	56	308	0.19
SD	19	78	0.08

*Data from U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, Md.

TABLE 2. Fall age-ratios indicated by deterministic simulations of the Rocky Mountain Canada Goose Population during the 1960-70s.

Numbers	Population Simulations*	
	Method I	Method II
Immatures (IM)	25,082	45,356
Adults (AD)	30,317	68,034
IM/AD in fall population	0.83	0.67
Corrected Number of Adults ^b	23,647	53,067
IM/AD expected in tail-fan survey	1.06	0.86

*Data from Table 40 of Krohn and Bizeau (1980:49).

^bNumber of adults decreased by 0.78 ($=1.00/1.29$) because immatures were 1.29 times more likely to be shot than adults (Krohn and Bizeau 1980:36).

vulnerable to shooting than immatures, then IM/AD ratios in the harvest should be approximately 0.86 to 1.06 (Table 2). If 77 percent of the immatures completed the tail molt during the hunting season, then from 19,313 ($=0.77 \times 25,082$) to 34,924 ($=0.77 \times 45,356$) immatures were misclassified as adults. Counting these misclassified immatures as apparent adults, the adjusted adult figures became 42,960 ($=19,313 + 23,647$) and 87,991 ($=34,924 + 53,067$). With

only 5,769 (=25,082 - 19,313) and 10,432 (=45,356 - 34,924) immatures with notched tail feathers remaining in the population, estimates of the observed tail-fan age ratios became 0.13 (= 5,769/42,960) and 0.12 (=10,432/87,911). Because it was likely that the 77 percent misclassification rate was high, we anticipated that these estimated ratios (0.12, 0.13) would be lower than the observed mean ratio (0.19).

Observed tail-fan age ratios became progressively lower from east to west (Table 3). The Pacific Flyway had the lowest mean age ratio, corresponding to the lowest percentage of birds from northern nesting areas. We suspect that the low age ratios in tail fans from the Pacific Flyway (excluding Alaska) was largely due to the harvest of more mid-latitude nesters (i.e., *B. c. hoffitti*), which presumably molt earlier relative to northern-nesting Canada geese.

TABLE 3. Tail-fan age ratios (immature:adult) of Canada geese as related to estimated percentages (n in thousands) of wintering birds from northern versus southern breeding areas.

Flyway and Population	Est. % of Wintering Birds, 1984-85, from: ^a		Tail-fan Age Ratios ($\bar{x} \pm SD$), 1982-86 ^b (Mean n per year)
	S. of 52° Lat.	N. of 52° Lat.	
Atlantic			
Northern U.S.A.	— (50) ^c	(764) —	
Total	6% (50)	94% (764)	0.96 $\pm$ 0.25 (3,047)
Mississippi			
Tennessee Valley	—	(130)	
Mississippi Valley	—	(477)	
Eastern Prairie	—	(168)	
Tallgrass Prairie	—	(197)	
Great Plains	(30) ^d	—	
Total	3% (30)	97% (972)	0.69 $\pm$ 0.26 (2,186)
Central			
Western Prairie	—	(135)	
Shortgrass Prairie	—	(194)	
Great Plains	(4) ^d	—	
Hi-Line	(93)	—	
Total	23% (97)	77% (329)	0.40 $\pm$ 0.07 (1,841)
Pacific			
Rocky Mountain	(90)	—	
Pacific	(50)	—	
Lesser	—	(150)	
Dusky	—	(8)	
Cackling	—	(23)	
Total	44% (140)	56% (181)	0.25 $\pm$ 0.11 (1,370)

^aData from Table 3 of Canadian Wildlife Service and U.S. Fish and Wildlife Service (1986:7); excluding Aleutian and Vancouver Canada geese because these populations are lightly hunted.

^bData from Table 18 of Sorensen *et al.* (1987:34-35).

^cAssumes 50,000 birds are resident geese (from unpubl. management plan, U.S. Fish and Wildlife Service, Washington, D.C.).

^dAssumes breeding population of 17,000 results in 34,000 wintering birds of which 30,000 winter in the Mississippi Flyway and 4,000 in the Central Flyway.

Discussion and Management Implications

Indirect evidence suggests that age ratios from tail fans of RMP geese, relative to the actual fall population, were biased low by a factor of 4 (0.2 vs. 0.7-0.8). Furthermore, the pattern of variation in tail-fan age ratios among flyways as related to the percentage of birds from northern versus southern breeding grounds is consistent with the hypothesis that, on a North American scale, latitude affects age ratios through time of nesting and molting. However, within a subspecies or population, factors other than latitude may affect time of molt. For example, Krohn and Bizeau (1980:22-23) noted that the start of egg laying in *B. c. moffitti* was related ($P < 0.01$) to altitude with up to a month difference in peak of nest initiation in sites at approximately 110 m (360 ft) above mean sea level versus those at 1,981 m (6,500 ft). This difference in time of nest initiation could result in a month or so difference in the start of molt between various flocks of *B. c. moffitti*. Thus, we concur with Hanson's (1965:118) statement that "It is advisable to consider both the nesting phenology and the characteristics of the individual populations before using collections of tail feathers to obtain age ratios."

Although it is clear that tail fan surveys do not accurately measure Canada goose age ratios, it does not necessarily follow that these ratios cannot be used as indices of recruitment. In the Eastern Prairie Population, Rusch (cited in Trost and Malecki 1985:503) found age ratios of harvested geese correlated with annual recruitment measured on the breeding ground. However, in the case of the RMP, tail-fan ratios may not be

useful recruitment indices given potentially variable molting chronologies resulting from a wide range of nesting elevations and spring weather conditions (i.e., yearly variation in the proportion of early- versus late-molting immatures could mask real changes in recruitment).

Tacha *et al.* (1987) questioned the continuation of tail fan surveys where *B. c. maxima* are harvested unless the bias associated with *B. c. maxima* can be eliminated or more reliable techniques developed. We agree with this concern over bias, but argue that even biased tail-fan ratios may provide useful recruitment indices. We recommend study of the timing and extent of molt in Canada geese, and whether or not tail-fan age ratios correlate with recruitment in specific populations. In addition to possibly solving the problem of reliable age determination from tails or other parts potentially submitted by hunters, this could also lead to better techniques for identifying subspecies and populations, longstanding needs for Canada goose management.

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Sequence of Trees Attacked by Spruce Beetles in a Mature Even-Aged Spruce Stand in South-Central Alaska

Abstract

Spruce beetles (*Dendroctonus rufipennis*) concentrate early attacks on an initial tree, the "focus" tree, but later attacks occur on adjacent trees, "recipient" trees. The pattern of these initial and following attacks may provide a key for management approaches to deal with spruce beetle outbreaks. Thus, this study was done to determine timing and distribution of spruce beetle attacks among trees in an unmanaged even-aged spruce stand. Repeated observations on 9 plots, each containing 10 formerly unfested spruce, revealed that the initially attacked trees ("focus" trees) were apparently moisture-stressed due to extensively frozen soils and rapidly warming air temperatures. Continued warm weather caused many more spruce beetles to emerge from hibernation and soils to thaw. Some newly emerged beetles attracted by odors from beetles already established in focus trees attacked the focus trees, but many attacked nearby unstressed trees ("recipient" trees). As a result, all focus trees and many recipient trees within 10 m of focus trees were killed. Furthermore, many recipient trees weakened by unsuccessful attacks were reattacked the following season. Knowledge of spruce beetle behavior that enables them to overwhelm the natural defenses of apparently unstressed trees in unmanaged stands should be useful to forest managers. Perhaps opportunities for spruce beetles to concentrate their attacks and kill clusters of trees could be reduced by partial forest harvesting to increase residual tree spacing. This should reduce competition among trees for soil moisture and should minimize stress at the beginning of the annual growth cycle when trees first become exposed to spruce beetle attack.

Introduction

Spruce beetle (*Dendroctonus rufipennis* (Kby.)) adults emerge from hibernation sites beneath the bark of dead and downed spruce (*Picea* spp.) in May and June (Schmid and Frye 1977). The beetles then disperse by flight when ambient temperatures exceed 14.5°C (Werner and Holsten 1985a), and females begin to attack new hosts. Attacks, which usually begin during the early period of rapid host growth, flowering, and pollination, are concentrated in the tree's lower bole (Knight 1960, Gara and Holsten 1975, Werner and Holsten 1985b, Hard 1987).

Many, if not all, *Dendroctonus* species produce aggregation pheromones after successful female entry into the host. These pheromones attract both additional beetles that assist in killing the first-attacked or "focus" tree and other beetles that attack nearby resistant and nonresistant "recipient" trees. The phenomenon of rapidly shifting mass attacks among trees, which commonly overwhelms trees singly and consecutively, is called "switching" (Geiszler and Gara 1978). Switching behavior may be driven by particular threshold concentrations of aggregation pheromones or by specific combinations of aggregation and antiaggregation pheromones, but the mode of operation differs among bark beetle species.

Some species produce antiaggregation pheromones, which apparently operate at a shorter range than attractant pheromones (Geiszler and Gara 1978, Berryman 1982), and prevent adverse competition among beetle broods by controlling attack density on hosts. The mountain pine beetle (*D. ponderosae* Hopk.), however, apparently also uses antiaggregation pheromone to force beetle attacks at higher densities on surrounding recipient trees than on focus trees (Geiszler and Gara 1978, Geiszler *et al.* 1980, Raffa and Berryman 1983). This behavior has presumably evolved to overwhelm the defenses of resistant recipient trees (Borden 1982).

Spruce beetles produce frontalin as an aggregation pheromone (Borden 1982) and methylcyclohexenone (MCH) as an antiaggregation pheromone (Rudinsky *et al.* 1974). To investigate switching behavior by the spruce beetle, Ford (1986) artificially baited spruce with frontalin. Results of his tests were inconclusive because focus trees and surrounding trees were attacked almost simultaneously, presumably because they were engulfed in strong attractant pheromone plumes.

In this study, data gathered for other purposes (Hard 1987) were reanalyzed to determine whether a) switching of attacks from focus trees to recipient trees was evident in a spruce stand being heavily attacked by spruce beetles in the

absence of artificial baits, b) attacks on recipient trees were greater than on focus trees, and c) recipient tree diameter or sapwood growth rate differed as distance of recipient trees from focus trees increased.

Study Area and Methods

The study area is near the junction of the Russian and Kenai Rivers at about 60°29' N, 149°58' W. Elevation of the site is about 130 m, slope ranges from 0 to 5 percent, and aspect is north. The stand that was monitored consisted of a virgin white spruce (*Picea glauca* (Moench) Voss) or Lutz spruce (*P. × lutzii* Little) stand about 135 years old at breast height (*bh*), but white spruce morphological traits predominated.

Nine variable-sized plots, each consisting of 10 contiguous uninfested spruce 20 cm in diameter at breast height (*dbh*) or larger with a few hardwoods and beetle-infested spruce interspersed, were established in early May of 1985. Trees had not yet begun their annual growth cycle and beetles were still in hibernation. Upper and lower margins of a 0.5-m bark sample strip encircling the stem near *bh* were marked with twine for subsequent counts of beetle attacks on each sample tree. Thermocouples were installed at 20-cm soil depth in three randomly located sites on each plot for weekly soil-temperature measurements, and a recording hygro-thermograph was installed near the center of the study area for measuring ambient air temperature and relative humidity.

Beginning on 4 June 1985, bark sample strips on all 90 sample trees were examined for new beetle attacks at alternating 3- and 4-day intervals until 20 August. New attacks were marked with staples at each sample visit, and numbers of attacks were converted to attacks per square meter of bark sample surface for each tree and sample interval. Two short increment cores, one from the east side and one from the west side at *bh*, were removed from each sample tree in late September after growth had ceased. The juncture of heartwood and sapwood was marked on each core, and cores were then stored and frozen in labeled plastic drinking straws for laboratory measurement of individual ring widths. Percentage of sapwood basal area growth at *bh* in 1984, the year before attack, was computed as an indicator of tree vigor (Münster-

Swendsen 1987) and potential resistance to beetle attack (Waring and Pitman 1985). Cores were cross-correlated visually using "marker" rings to determine whether each tree had formed a new xylem ring at *bh* in 1985 because trees that are mass-attacked very early in the season are sometimes unable to develop even a portion of a new annual ring in the lower bole.

Approximate geographic center of each plot was marked and azimuth and distance to each sample tree were measured for preparation of plot maps. The tree or trees that were apparently attacked earliest on each plot and then mass-attacked most rapidly by spruce beetles were labeled as initial plot "focus trees." This procedure provided the best estimate of which trees were attacked first, but accuracy was limited by the 3- and 4-day sample interval. Concentric arcs or circles representing 5-m and 10-m distances from focus trees were drawn on each plot map for segregation of sample trees into concentric sample bands.

Results

Spruce beetle attacks began on 14 June 1985 but did not increase rapidly until after 21 June (Figure 1a). Total attacks on all sample trees peaked on 2 July (Figure 1a), but attacks had begun from 1 to 2 weeks earlier on focus trees (Figures 1a and 2a).

Two of the nine plots each had two widely-separated focus trees that were apparently attacked simultaneously. One plot had two widely-separated focus trees that were not attacked simultaneously but were attacked earlier than surrounding trees. Remaining plots each had one focus tree. Heavy attacks on focus trees occurred as mean maximum air temperatures exceeded the lower threshold temperature for spruce beetle flight (Figure 1b). Mean soil temperature at the study site increased markedly above freezing (Figure 1c) after most focus trees were initially attacked (Figure 2a). Therefore, focus trees were successfully attacked during a period of apparent host-moisture stress, indicated by temporarily slowed tree expansion rates, that was widespread throughout the study area (Hard 1987). Soil moisture bound in still-frozen mineral soil was not available for increased transpiration by many trees exposed to low precipitation, rapidly increasing air temperatures, and slowly increasing soil temperatures.

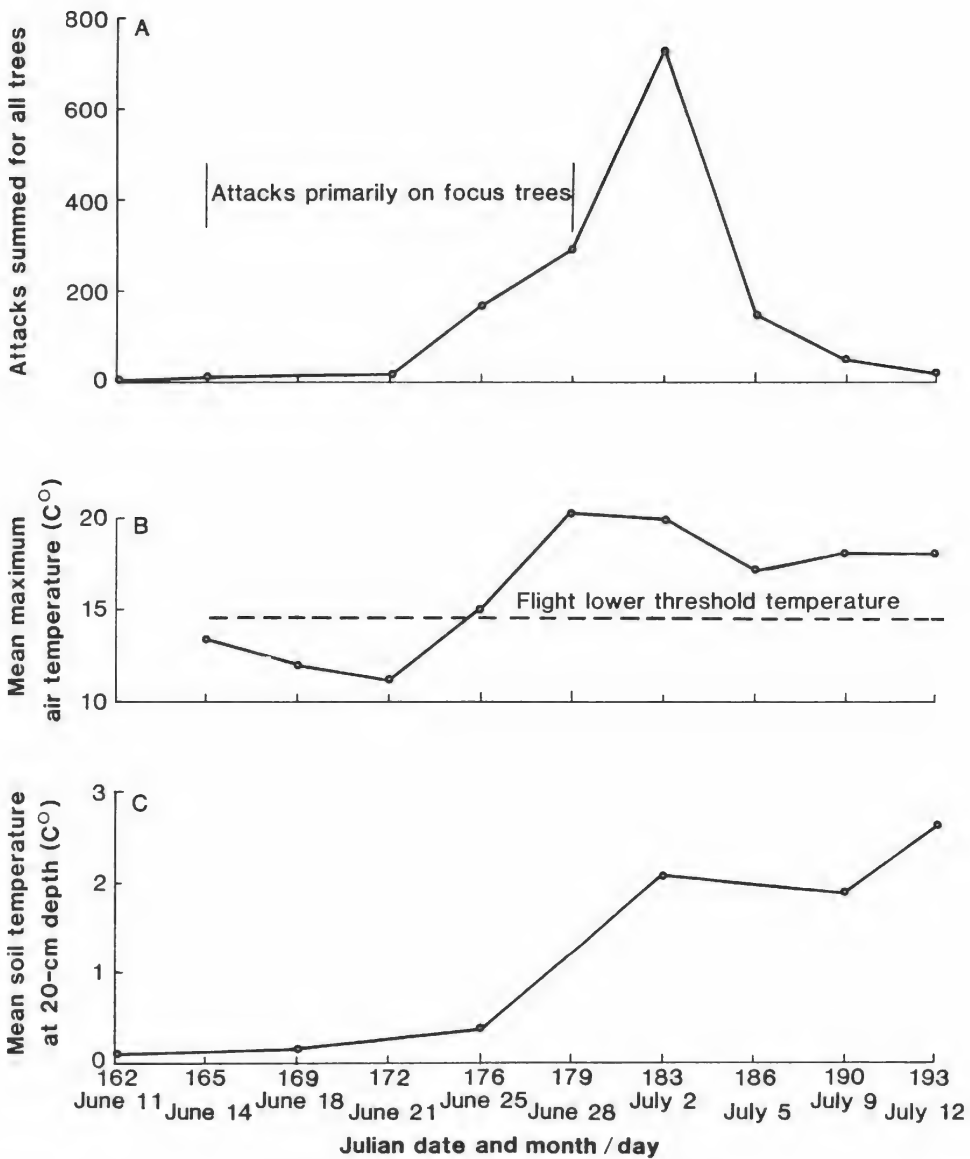


Figure 1. A. Spruce beetle attacks summed by sample interval for all sample trees. B. Mean maximum air temperature within the sample stand by sample interval. C. Mean soil temperature by alternate sample interval.

Mean Julian date when attacks were first observed increased from attack of focus trees to attack of trees in the outermost concentric sample band, but the greatest time delay of mean

initial attack between concentric samples occurred between focus trees and trees within the adjacent sample band (Figure 2a). All focus trees were killed, and mean percentage of recipient

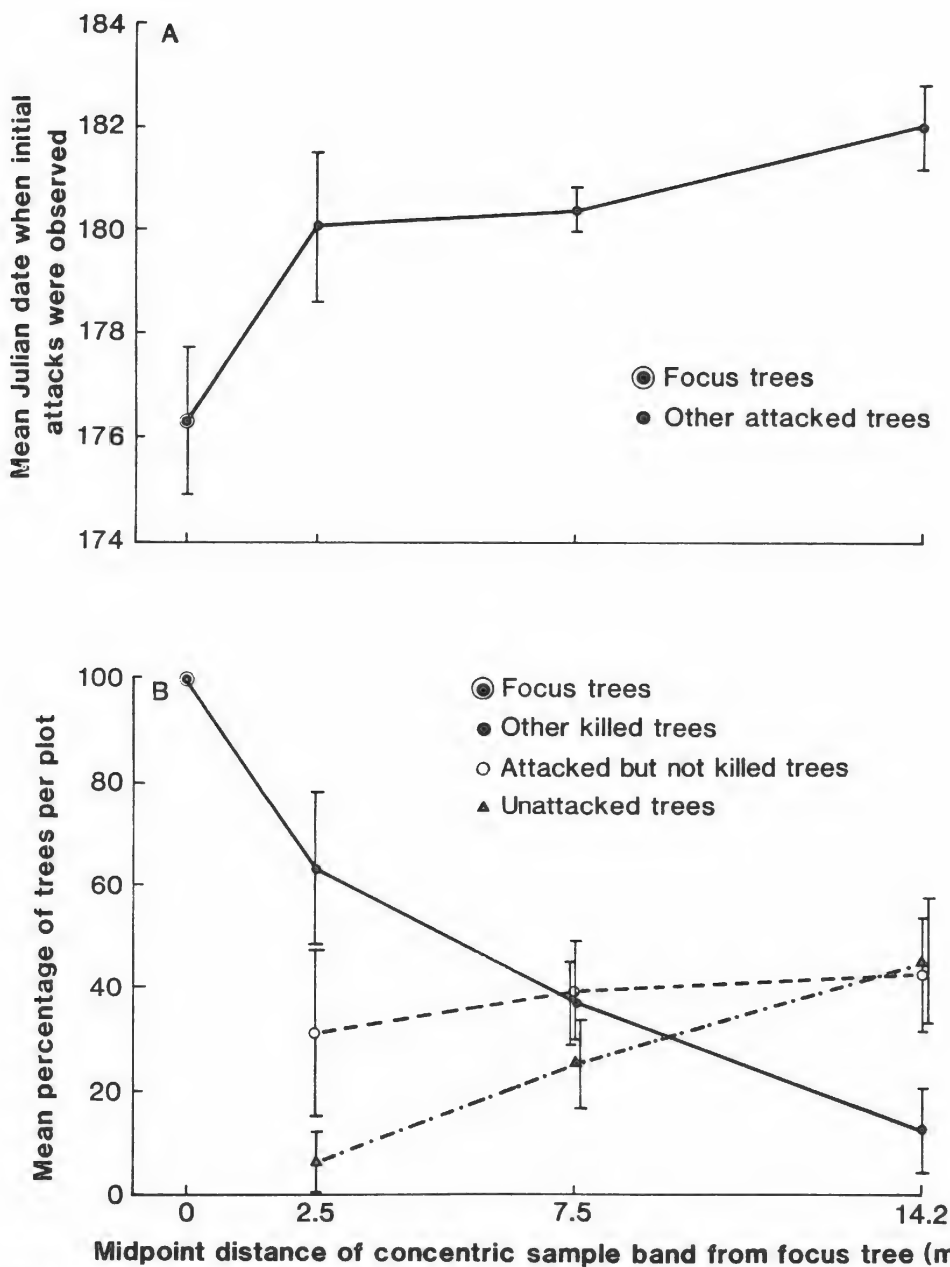


Figure 2. A. Mean Julian date when spruce beetle attacks were first observed on focus trees and on recipient trees in concentric sample bands. B. Mean percentage of sample trees that were killed, attacked and unkilld, or unattacked over mid-distance of concentric sample bands from focus trees. Vertical bars equal ± 1 standard error.

trees that were killed decreased as distance from focus trees increased (Figure 2b). Mean percentage of recipient trees that were attacked but not killed or trees that were unattacked increased as distance from focus trees increased.

Mean total numbers of attacks at *bh* and peak mean daily attacks decreased as the Julian date when attack densities peaked increased (Figure

3). Mean total numbers of attacks at *bh* decreased generally from focus trees to surrounding trees (Figure 4). Killed trees were usually attacked more heavily at *bh* than attacked but unkilld trees. Neither mean *dbh*'s of attacked trees nor mean percentages of sapwood area growth of attacked trees differed significantly as distance of recipient trees from focus trees increased (Figures 5a and b).

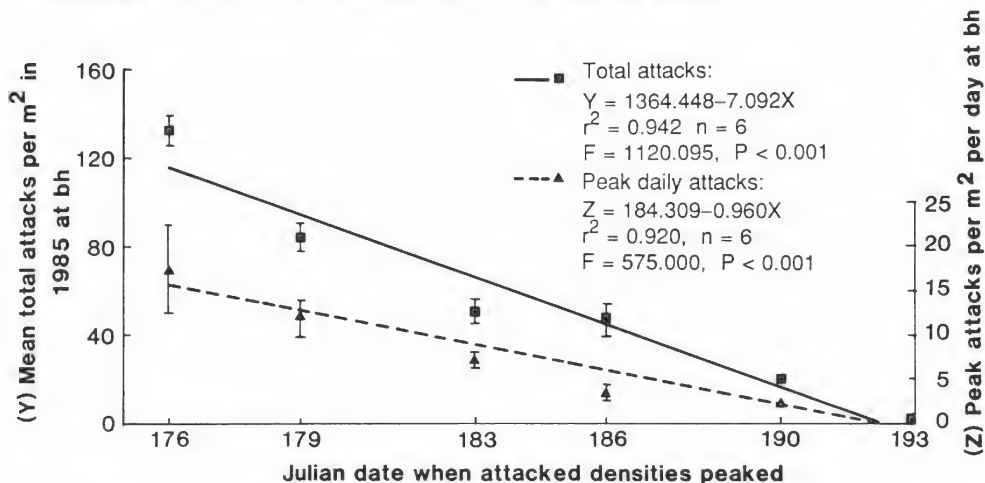


Figure 3. Mean total spruce beetle attacks in 1985 (Y) and peak mean daily attacks (Z) relative to Julian date when attack densities peaked. Vertical bars equal ± 1 standard error.

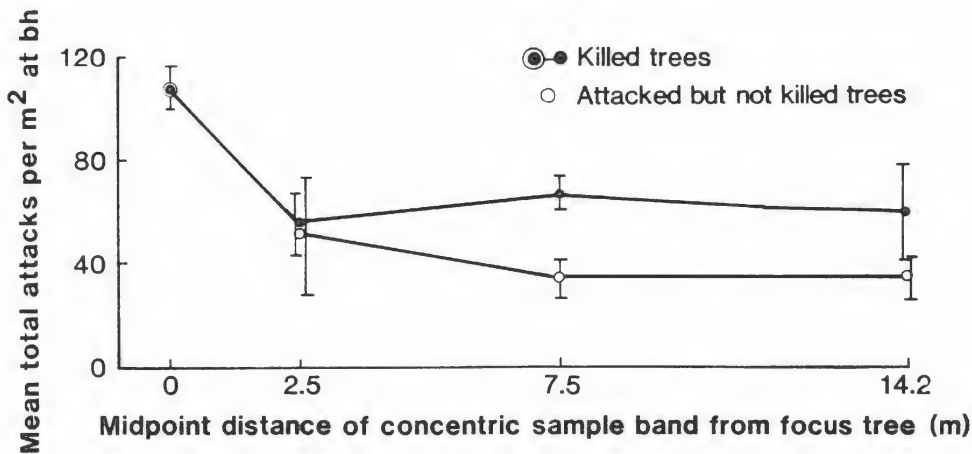


Figure 4. Mean total numbers of spruce beetle attacks per square meter on focus trees and on trees in concentric sample bands. Vertical bars equal ± 1 standard error.

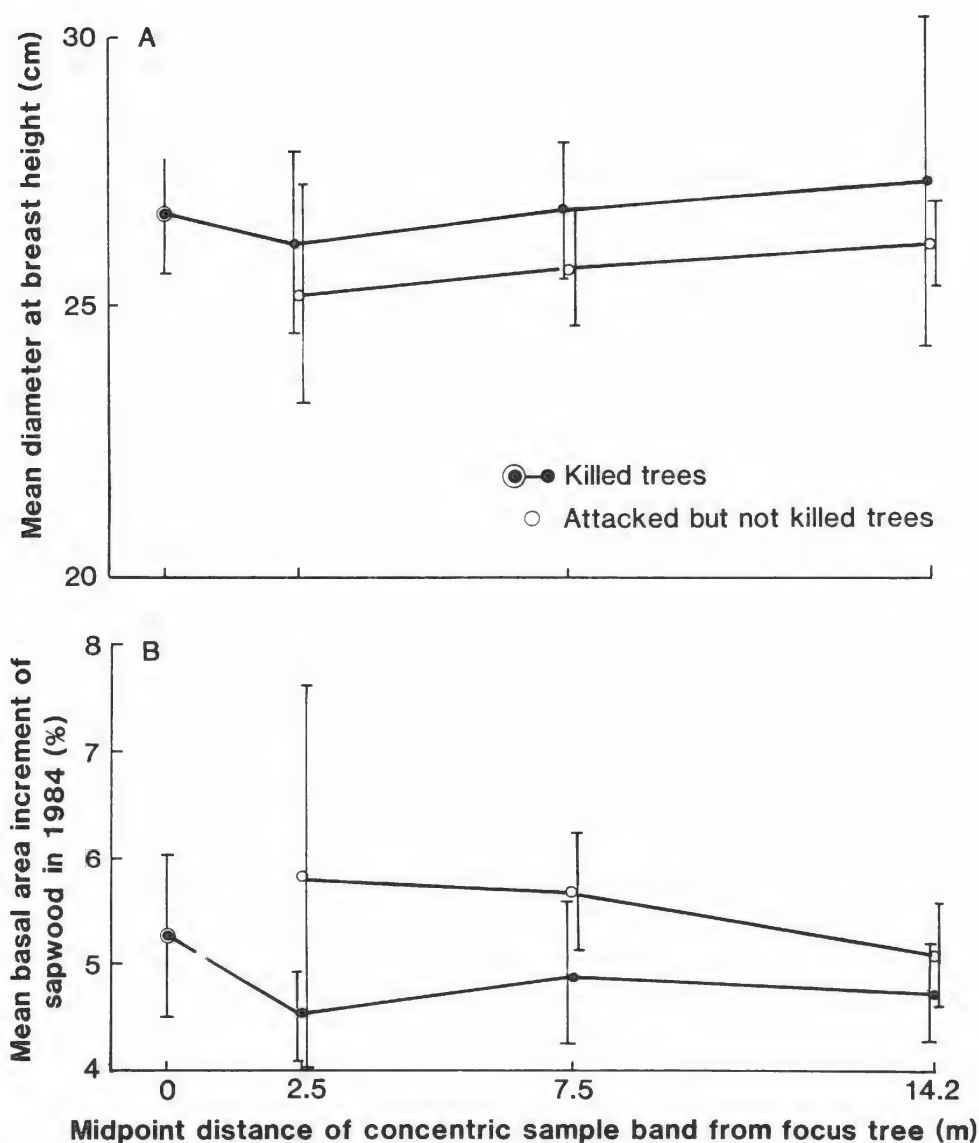


Figure 5. A. Mean *dbh*'s of focus trees and attacked trees on concentric sample bands. B. Mean percentages of sapwood basal area increment of focus trees and attacked trees on concentric sample bands. Vertical bars equal ± 1 standard error.

The ratio of width of xylem ring formed in 1985 to width of ring formed in 1984 decreased as number of beetle attacks at *bh* increased (Figure 6). Narrow xylem rings formed in heavily attacked trees may reflect earlier interruption of radial growth compared to growth in lightly at-

tacked and unattacked trees because some photosynthates normally used for respiration and stem radial growth are used for tree defense instead.

Reduced ratios of attacked trees paralleled reductions in bole expansion rates after tree attack by spruce beetles (Hard 1987). Many of the

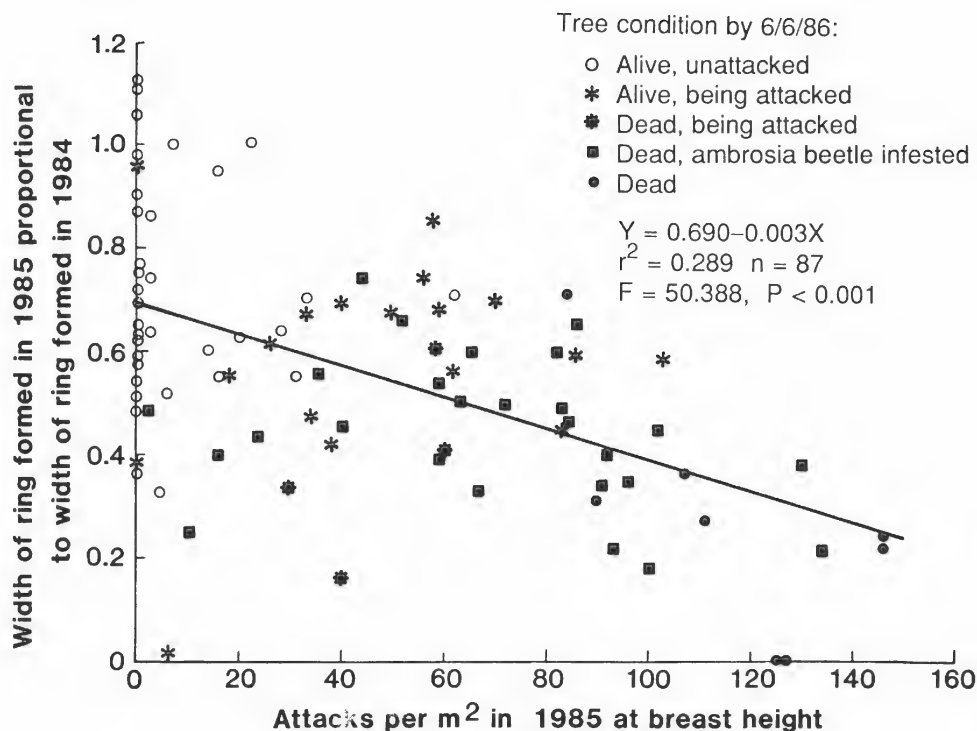


Figure 6. Width of xylem ring formed in 1985 proportional to width of xylem ring formed in 1984 relative to spruce beetle attacks per square meter in 1985.

trees that died during the winter of 1985-86 were attacked by ambrosia beetles (*Trypodendron* sp.) in the late spring of 1986, whereas many trees that survived 1985 spruce beetle attacks were reattacked by spruce beetles in 1986.

Discussion

The few trees attacked first appeared to serve as foci for attacks on nearby trees. Attacks continued on focus trees after recipient trees were attacked, however, and mean total attacks on recipient trees were less than on focus trees. Apparently, the "repelling model" of switch attack behavior characteristic of mountain pine beetles (Geiszler *et al.* 1980) is not characteristic of the spruce beetle because higher attack rates did not occur on surrounding resistant trees. The "threshold model," first termed by Geiszler *et al.* (1980) to label descriptions of switching by the southern pine beetle (*D. frontalis* Zimm.) (Coster

and Gara 1968, Gara and Coster 1968), appears to be more characteristic of the spruce beetle.

Spruce beetles concentrate attacks in localized areas around focus trees, presumably because strong attractant pheromone plumes form around focus trees. Nonresistant trees are often killed, but less concentrated attacks in apparently resistant trees may convert them to a less resistant state for attack the following year. This appears to be an effective but less aggressive manner of colonizing resistant hosts than that used by the mountain pine beetle (Geiszler and Gara 1978, Raffa and Berryman 1983).

Tree survival appears to depend primarily on attack density, and attack density appears to depend largely on early occurrence of initial attack, rapidity of mass attack, and length of time that a tree undergoes attack. Neither *dbh* nor percentage of sapwood basal area increment of recipient trees appeared to differ as distance from focus trees increased.

Artificial baits or artificially high concentrations of bait that could cause abnormal beetle behavior were not used in this study. Factors that control spruce beetle switch-attack behavior could have been obscured, however, by the twice-weekly sampling regime.

Further studies using a shorter sample interval are needed to clarify the antiattractant func-

tion of MCH. Details of its role in the switching of attacks by spruce beetles from focus trees to recipient trees remain unclear.

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Avian Community Changes Following Lower Granite Dam Construction on the Snake River, Washington

Abstract

The reservoir behind the Lower Granite Dam on the Snake River inundated 210 ha of riparian habitat and 1109 ha of flood plain habitat. Loss of these habitats was associated with the change from free-flowing river to reservoir. Our objective was to evaluate responses of the avian community to habitat change. We compared numbers of birds and species observed during monthly road counts in 1973 (preimpoundment) and 1981 (postimpoundment). More individual birds and species per survey were observed in 1981. Of 37 species classified as riparian, 18 had a larger number of individuals observed in 1981. Our data suggest that some riparian species shifted habitat-use patterns after impoundment, and/or that nonriparian upland habitats were not adequately surveyed prior to impoundment. Riparian passerines decreased after impoundment in number of individuals and species per survey, and may not have been dependent on riparian habitat. More individuals and eight new species of aquatic birds were recorded in 1981. Migrant ducks during spring contributed heavily to the increase in aquatic birds. The proportion of total birds observed increased for aquatic and upland birds and decreased for riparian birds. These changes paralleled changes in habitat behind the dam. This study may aid in evaluating environmental impacts caused by impoundments.

Introduction

Lower Granite Dam (LGD) on the Snake River in southeastern Washington was completed in 1975, and inundated 210 ha of riparian and 1109 ha of flood plain habitat (Lewke and Buss 1977). Riparian habitat is important to many bird species (Walcheck 1970, Thomas 1979). Because of changes in habitat behind LGD, Lewke and Buss (1977) predicted that bird species dependent on riparian habitat would decrease.

Associated with loss of riparian habitat was the change from free-flowing river to a 63 km long reservoir. Weber and Larrison (1977) observed that reservoirs along the Snake River were attracting certain marine birds uncommon in the area before impoundments. Thus, species that use aquatic habitat were expected to increase after impoundment.

Our objective was to evaluate avian community changes behind LGD. We compared numbers of individuals and species observed during monthly road counts in 1973 (preimpoundment) (Lewke 1975) with data collected in 1981 (postimpoundment).

Study Area

We collected data between Steptoe and Wawawi canyons, along the lower Granite Reservoir in

southeastern Washington during 1973 and 1981. In 1981, riparian habitat was limited to draws and small isolated areas along the reservoir. The canyon walls are steep and lined with basalt cliffs. A road follows the north side of the reservoir. Most upland habitat is grassland; dominated by cheat grass (*Bromus tectorum*) and bluebunch wheatgrass (*Agropyron spicatum*). An overstory of rabbit-brush (*Chrysothamnus nauseosus*) occurs in some places. Dominant riparian vegetation is poison oak (*Rhus radicans*), blackberry (*Rubus discolor*), snowberry (*Symphoricarpos albus*), hackberry (*Celtis reticulata*), and white alder (*Alnus rhombifolia*). For a preimpoundment description of the study area see Lewke and Buss (1977).

Methods

Road count methods followed Lewke (1975) and were conducted between the twelfth and seventeenth of each month. Surveys were initiated within 30 minutes of sunrise. Counts were conducted between Steptoe and Wawawi canyons and direction of travel alternated each month. In 1973, the route was along the river and bordered riparian vegetation and flood plain; this road was inundated by the reservoir. The road used in 1981 was along the reservoir where it passed through grasslands and often was adjacent to basalt cliffs. In both years, the road was along the north side of the reservoir. Thirty-three

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stations were located along the route at 0.8 km (0.5 mile) intervals. All birds heard or seen within a 0.4 km (0.25 mile) radius (ocular estimation) at each station were recorded during a three-minute observation period. Only birds north of the reservoir's south shore were recorded (including flying and swimming ducks and soaring hawks [Lewke 1975]). Observations were made with 10x binoculars or 15-60x spotting scope.

Bird species were placed into habitat and residency categories. Habitat categories included: riparian species (those that used riparian habitat proportionally more than it was available on the study area [Lewke and Buss 1977]) (e.g., black-capped chickadees [*Parus atricapillus*], warblers, and dark-eyed juncos [*Junco hyemalis*]); aquatic species (those that use predominately aquatic habitat (e.g., grebes, ducks, and gulls); upland species (those not classified as riparian or aquatic) (e.g., swallows, common raven [*Corvus corax*], and western meadowlark [*Sturnella neglecta*]). Weber and Larrison (1977) was consulted to aid in classification of birds into the following residency categories: permanent resident, summer resident, winter resident, and

migrant. Avian nomenclature follows American Ornithologists' Union (1983).

We used the Wilcoxon paired-sample test (Zar 1984) to compare number of individuals and species richness (number of species) observed per survey (12 surveys per year) between 1973 and 1981. Hypotheses for these tests were that values in 1973 are $\geq$, $\leq$, or $=$ to values in 1981.

We used Chi-square contingency table analysis (Zar 1984) to test if the proportion of individuals and species observed in each residency and habitat category changed between years. A separate test was made within each category.

Results

Mean monthly temperatures were similar between 1973 and 1981 (N.O.A.A. 1973, 1981). Annual rainfall was slightly higher in 1981 (36.09 cm) than 1973 (31.42 cm). Precipitation levels were similar in all seasons except summer, which was drier in 1973 (0.69 cm) than in 1981 (7.30 cm).

Numbers of individuals per survey were greater in 1981 ($P = 0.10$) (Figure 1). More individuals were observed during every month in

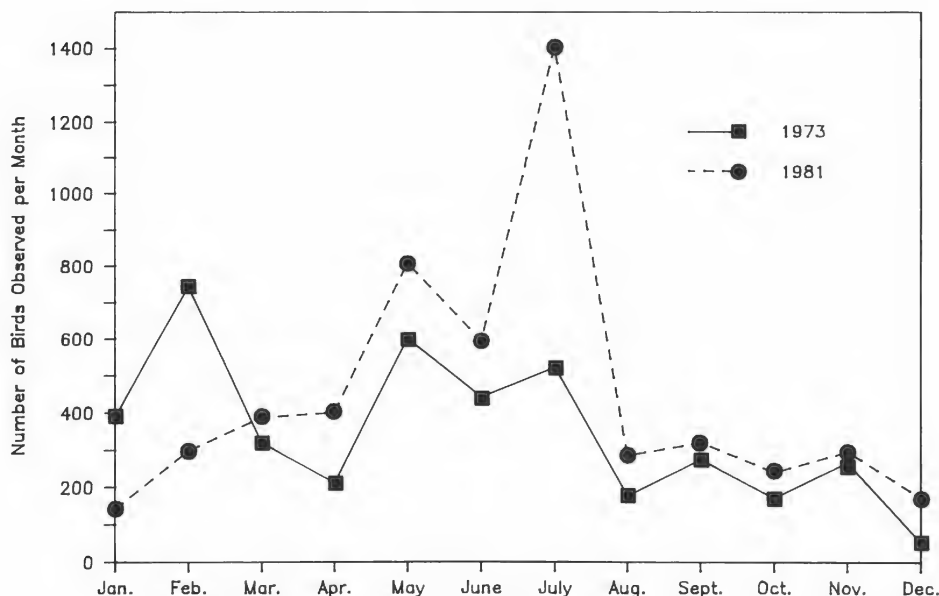


Figure 1. The number of avian individuals observed for all species during monthly road counts, behind the Lower Granite Dam along the Snake River in southeastern Washington, 1973 (preimpoundment) and 1981 (postimpoundment).

1981, except January and February (Figure 1). Numbers of species per survey also were greater in 1981 ($P = 0.03$). Differences in species/month between years were somewhat erratic, but changes were small in months where species richness was greater in 1973 (Figure 2).

Habitat Categories

In the aquatic habitat category, numbers of individuals per survey were greater in 1981 ($P = 0.05$). Differences between years were relatively minor in most months, except in April and May when large numbers of aquatic birds were observed in 1981. The numbers of aquatic species per survey were larger in 1981 ($P = 0.001$), differences were largest during April and May. Only in August, when aquatic birds were uncommon on the study area, was a larger number of aquatic species observed in 1973.

Differences did not occur for birds in the riparian category for number of individuals ($P = 0.32$) or species ($P = 0.40$) per survey. However, division of riparian birds into passerines and nonpasserines revealed important dif-

ferences. Riparian passerines decreased in 1981 for individuals ($P = 0.08$) and species ($P = 0.02$) per survey. The largest monthly decreases in riparian passerine birds occurred in January and February. These were the only two months where the total number of individuals of all birds observed was larger in 1973 (Figure 1). The numbers of individuals and species in riparian passerines also were much smaller during the summer. Nonpasserine riparian birds per count increased for both individuals ($P = 0.08$) and species ($P = 0.01$) per survey.

Upland birds increased in both the number of individuals ($P = 0.08$) and species ($P = 0.02$) per survey. Cliff swallows (*Hirundo pyrrhonta*) in June and July increased notably (419 vs. 1442). Increases in this species caused July of 1981 to have the largest number of individuals observed for any month for both years. (Figure 1).

Residency Categories

Permanent residents increased from 1973 to 1981 in both numbers of individuals ($P = 0.05$) and

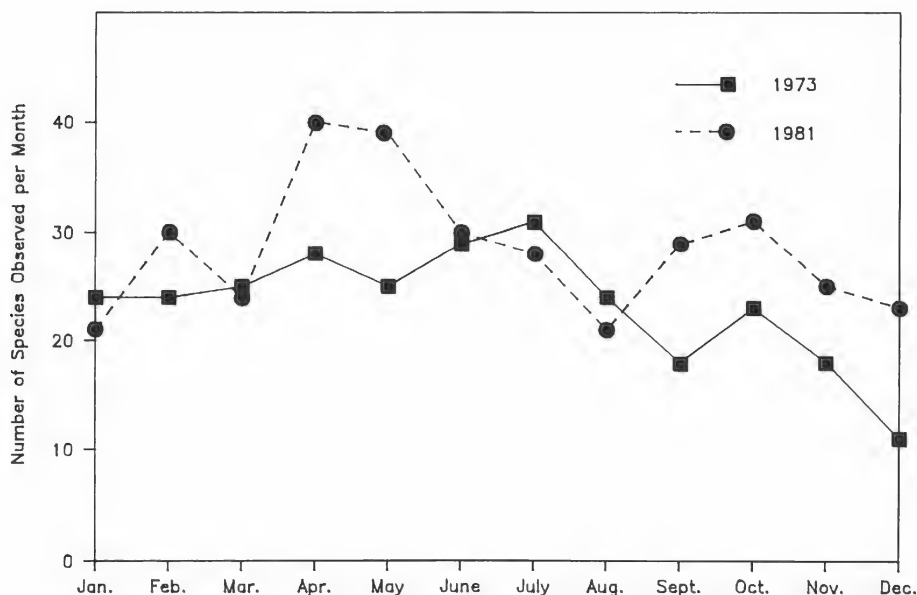


Figure 2. The number of avian species observed during monthly road counts, behind the Lower Granite Dam along the Snake River in southeastern Washington, 1973 (preimpoundment) and 1981 (postimpoundment).

species ($P = 0.002$) per survey. No month had more permanent resident species in 1973 and only in January and February were less individuals observed in 1981.

Paralleling the decrease in permanent residents during winter was a decrease in winter resident individuals per survey ($P = 0.06$). However, the numbers of winter resident species per survey were not different between years ($P = 0.38$).

More migrant species per survey were observed in 1981 ($P = 0.02$), but individuals per survey were not different between years ($P = 0.25$). The increase in migrant species richness was predominately due to waterfowl, particularly in spring. Unlike the other resident categories, we did not detect a significant difference for summer residents in number of individuals/month ($P = 0.28$) or species/month ($P = 0.34$).

Proportion of Each Category to Yearly Totals

Proportion of species in each habitat and residency category, relative to total species observed in each year, remained constant for each category ($P > 0.10$) (Table 1). Proportion of individuals observed (Table 1) changed in every category ($P < 0.001$) except permanent residents ($P = 0.42$). Proportion of individuals observed increased for aquatic birds, upland birds, summer residents, and migrants. Proportion of individuals observed for riparian birds and winter residents decreased.

Discussion

Lewke and Buss (1977) estimated that the LGD reservoir inundated 210 ha of tree-shrub riparian habitat. Little riparian habitat was present in 1981, relative to what was present in 1973. Lewke (1975) classified species as riparian dependent, based on a species being observed in riparian habitat proportionally more often than that habitat was available. Use and availability data are commonly used to detect habitat selection or preference by bird species (e.g., Holbrook *et al.* 1987, Wilson and Crawford 1987, Thompson and Baldassarre 1988). Of 37 species classified as riparian in this study, 18 had a larger number of individuals observed in 1981. Increases were particularly large for five of these species: American kestrel (*Falco sparverius*) (16 in 1973 to 59 in 1981), chukar (*Alectoris chukar*) (165 in 1973 to 401 in 1981), rock dove (*Columba livia*)

TABLE 1. Yearly totals for species richness and number of individuals by habitat and residency categories, from road counts along the Snake River in southeastern Washington, 1973 (preimpoundment) and 1981 (postimpoundment).

Categories	Species		Individuals	
	1973	1981	1973	1981
Habitat categories				
Aquatic	14	22	292	593*
Riparian	32	30	2364	2114*
Upland	17	22	1505	2655*
Annual Total	63	74	4161	5362
Residency categories				
Permanent residents	29	33	2327	2986
Summer residents	19	19	1250	2111*
Winter residents	8	9	536	91*
Migrants	7	13	48	174*
Annual Total	63	74	4161	5362

*The proportion of the category to the annual total in 1973 < 1981 ($P < 0.001$).

*The proportion of the category to the annual total in 1973 > 1981 ($P < 0.001$).

(62 in 1973 to 275 in 1981), black-billed magpie (*Pica pica*) (168 in 1973 to 279 in 1981), and European starling (*Sturnus vulgaris*) (201 in 1973 to 397 in 1981). These species use talus slopes and cliffs extensively (Thomas 1979, Brown 1985), which were common along the study route in 1981. We suggest three possible causes for the increases: 1) species increased after impoundment, 2) species shifted habitat use patterns after impoundment causing an increased detection and/or 3) talus slope and cliff habitats were not adequately surveyed prior to impoundment. These species may have selected or preferred riparian habitat prior to impoundment, but their dependency on it is questionable.

The road used in 1973 bordered riparian habitat along the river. In 1981 the relocated road was adjacent to talus slopes, basalt cliffs, and grassland along the reservoir. Changes in the habitat surveyed may have contributed to apparent increases in the following upland species: gray partridge (*Perdix perdix*) (0 in 1973 and 26 in 1981), rock wren (*Salpinctes obsoletus*) (126 in 1973 and 266 in 1981), and western meadowlark (196 in 1973 and 278 in 1981). These species

were associated with upland habitat (Thomas 1979, Brown 1985) along the survey route in 1981.

Riparian passerines may have been dependent on riparian habitat, as reflected by decreases in number of individuals and species per month. Riparian passerines that contributed largely to this decrease were the lazuli bunting (*Passerina amoena*) (52 in 1973 to 2 in 1981), white-crowned sparrow (*Zonotrichia leucophrys*) (320 in 1973 to 14 in 1981), dark-eyed junco (132 in 1973 to 19 in 1981), house finch (*Carpodacus mexicanus*) (153 in 1973 to 28 in 1981), and American goldfinch (*Carduelis tristis*) (441 in 1973 to 76 in 1981).

Many aquatic birds increased and eight new aquatic species were observed in 1981. Migrant ducks contributed to the annual increase in aquatic species and individuals. These ducks may have been attracted to the reservoir for rest stops during migration.

Aquatic birds were not common during summer months before or after impoundment. However, the number of individuals observed decreased between years for July and August. These data indicate that this area received limited use by aquatic species for nesting and raising young, both before and after impoundment. Water level fluctuations associated with dam operation may inhibit waterfowl nesting (McCabe 1979, Books 1985). Other than the increase in cliff swallows, only small differences were observed for the summer months in species richness and number of individuals (Figure 1 and Figure 2), indicating that the impoundment had little effect on total avian breeding community along the river. However, it is clear that riparian passerines were fewer in species and less common during the breeding months.

The only aquatic species to suffer a large decline was the common goldeneye (*Bucephala clangula*) (79 in 1973 to 27 in 1981). Goldeneyes

may prefer river over reservoir habitat, because they were frequently observed on the river above the reservoir where the current was more swift. The decrease in goldeneyes indicates that increased water-surface-area and slowing of the flow-rate may not have benefited all aquatic species.

The reservoir appears to benefit aerial insectivores, possibly because of an increase in invertebrates associated with the larger water surface area. The following swallow species were observed only in 1981: tree swallow (*Tachycineta bicolor*), violet-green swallow (*T. thalassina*), northern rough-winged swallow (*Stelgidopteryx serripennis*), and barn swallow (*Hirundo rustica*). Numbers of Say's phoebe (*Sayornis saya*), eastern kingbirds (*Tyrannus tyrannus*), and cliff swallows were all larger in 1981.

Road-counts do not yield density estimates, but they are an index to relative changes in species abundance (Rotenberry 1982). This study represents only two years of data and to perceive these years as typical for preimpoundment and postimpoundment bird populations may not be prudent. The increase in the proportion of aquatic and upland birds, and the decrease in the proportion of riparian birds paralleled the changes in habitat available.

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Relations Between Site Index, Salal, Plant Communities, and Sites in Coastal Douglas-fir Ecosystems

Abstract

Salal is often considered an undesirable forest plant in coastal British Columbia and is thought to have adverse effects on tree growth. To assess the relationship between salal cover and tree growth in southwestern British Columbia, vegetation data from 101 sample plots in disturbed immature Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] plantations were analyzed. This analysis indicated that the plots could be placed into one of five vegetation units. To eliminate non-plant influences on Douglas-fir growth, plots with the same climatic, soil moisture, and soil nutrient regimes in two vegetation units where salal was most and least abundant, were selected for detailed analysis. This analysis indicated that there were no significant differences between the two sets of plots in Douglas-fir foliar nutrients despite the fact that one set had high cover and the other low cover of salal. Furthermore, regression analyses indicated a poor relationship between site index and salal cover suggesting that salal cover had no major adverse effect on Douglas-fir height growth. When data from all the study plots were analyzed, it was found that variables representing the soil moisture or nutrient regimes were better predictors of site index than were various vegetation variables, not involving salal cover. Salal cover was a poorer predictor of site index than any of these variables. It is concluded that salal may not necessarily significantly influence tree growth in the ecosystems studied.

Introduction

Classification of forest lands according to ecological site quality is recognized as being essential for sound forest management. Recent efforts have attempted to (a) identify ecological variables controlling forest productivity and (b) use these variables to estimate potential productivity of crop trees on different sites. This study examines relationships of vegetation and sites to site index in coastal Douglas-fir ecosystems by applying the methods of biogeoclimatic ecosystem classification (Pojar *et al.* 1987), with particular attention to salal (*Gaultheria shallon* Pursh).

The influence of salal on tree growth has attracted considerable research attention in coastal British Columbia resulting in the development of the Salal-Cedar-Hemlock Integrated Research Program (W. W. Bourgeois, pers. comm.). Field observations, surveys, and studies in the Wet or Very Wet, Hypermaritime or Maritime Coastal Western Hemlock subzones have indicated that the growth performance of crop tree species in salal-dominated plantations, and immature and old-growth stands is very poor (e.g., Lewis pers. comm., Germain 1985, Weetman *et al.* pers. comm.). Where sites have been burned and planted, tree growth has improved; similarly, dense, naturally regenerated, immature stands that developed after disturbance by wind or harvesting feature rapid growth rates and a nearly complete absence of salal.

An ecological parallel between the growth stagnation in salal-dominated and other ericaceous species-dominated ecosystems, e.g., *Calluna*-ecosystems in Britain (Malcolm 1987) and *Kalmia*-ecosystems in eastern Canada (Daman 1971), has been suggested by G. F. Weetman (pers. comm.). As there is some evidence of an adverse, direct or indirect, influence of ericaceous plants on forest productivity, foresters in coastal British Columbia consider the presence of salal undesirable and expect treatments that eradicate the species are likely to improve forest growth.

This study examines (1) the possible effect of salal on the stand and soil nutrient status and site index and (2) the relations between site index, salal, plant communities, and sites in disturbed, immature, coastal Douglas-fir ecosystems. These objectives are accomplished by comparing vegetation and environmental characteristics of 101 ecosystems and through the use of analysis of variance and regression analysis. Differences in foliar and soil nutrient characteristics and site index between stands with high and low salal cover are examined on a population of 30 biologically-equivalent ecosystems with the same climatic, soil moisture, and soil nutrient regimes. The authors recognize that, when stands of different vegetation are compared on similar sites, the question always remains whether differences in productivity are due to differences in vegetation

changes, or manifest original differences in site quality.

Study Area

All study ecosystems were located within the Very Dry Maritime CWH (CWHxm) subzone on eastern Vancouver Island and the Dry Maritime CWH (CWHdm) subzone on the adjacent mainland (Carter and Klinka 1988). This area is characterized by a very dry (CWHxm subzone) to dry (CWHdm subzone) maritime cool mesothermal climate and it is underlain by volcanic rocks (Vancouver Island) or granitic rocks (coastal mainland). Glacial till is the most common landform, although fluvial or marine deposits are frequently encountered. Soils are typically coarse-textured (loamy-sand to sandy-loam) Humo-Ferric Podzols (Canada Soil Survey Committee 1978). Most soils have a high content of coarse fragments and are acidic with acidity decreasing with depth.

Old growth forests are usually dominated by western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Douglas-fir with significant amounts of western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.). Second growth forests are usually dominated by naturally regenerated or planted Douglas-fir. A high cover of ericaceous species (e.g., *Gaultheria shallon* Pursh and *Vaccinium parvifolium* Sm. in Rees) and acidiphilous mosses [e.g., *Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregana* (Sull.) Ochyra, *Plagiothecium undulatum*, (Hedw.) B.S.G., and *Rhytidiadelphus loreus* (Hedw.) Warnst.] are the characteristic floristic features of zonal ecosystems. A more complete description of the study area is given by Carter and Klinka (1988).

Materials and Methods

The study stands were all plantations and part of a larger fertilization study (Carter and Klinka 1988). The stands were dominated by Douglas-fir, even-aged with a relatively narrow range in age (18 to 43 years), stocking (400 to 880 stems/ha), and free of disease and insect problems. All study stands had a similar management history following the harvest of old growth stands: slashburning, planting to Douglas-fir of various coastal seed sources, and spacing treatment.

Sample plots within these stands were chosen to represent the major segments of the soil

moisture and soil nutrient gradients present in the CWHxm and CWHdm subzones. In each stand a 20 × 20 m plot (0.04 ha) was selected to represent an individual ecosystem relatively uniform in understory vegetation and soils.

Vegetation, topography, and soils of each plot were described using a simplified version of the standard procedure employed by Ecological Program Staff of the B.C. Forest Service (Walmsley *et al.* 1980). The cover of all species present in the shrub, herb, and moss layers was estimated visually using the species significance scale (Mueller-Dombois and Ellenberg 1974). Species growing exclusively as epiphytes, on decaying wood, and/or coarse fragments/rocks were not included in the analysis. Soil moisture and nutrient regimes were identified in the field using the methods described by Klinka *et al.* (1984) and Carter and Klinka (1988). Forest floors and soils were described and identified according to Klinka *et al.* (1981) and Canada Soil Survey Committee (1978) respectively. Site index was calculated using Bruce (1981) with measurements of age and height for not less than 30 dominant and codominant trees per stand.

Sample plots were classified using the methods and system of biogeoclimatic ecosystem classification as described by Pojar *et al.* (1987). The classification was based on plant species present in the understory stratum, using tabular comparisons (Westhoff and van der Maarel 1980), diagnostic criteria (Pojar *et al.* 1987), and VTAB tabling program (Emanuel pers. comm.). To examine consistency of groupings obtained from the tabular comparisons, multivariate analysis of vegetation was conducted using principal components analysis (Fox and Guire 1976), and the ORDIFLEX program of Gauch (1977). PCA was performed on a correlation matrix (Noy-Meir and Whittaker 1977), using only those species included in the diagnostic table.

On each plot the current year's foliage from the upper crown of 15 dominant or codominant trees was sampled in October, and analyzed for total N, P, K, S, SO₄-S, Ca, Mg, "active" Fe, Mn, Cu, Zn, and B following the guidelines and procedure given by Ballard and Carter (1986). The same guidelines were used to evaluate forest stand nutrient status using concentrations (dry-mass basis) and total content (milligrams per 100 needles).

On the 56 sample plots forest floor and mineral soil physical and chemical properties were examined and sampled separately at five random sampling points in each of these plots. Composite samples of forest floor and composite bulk samples of 0-30 cm mineral soil were taken from three points of an equilateral triangle (2 m on a side), located over each point. Bulk density was measured near the point from which each soil sample was collected by cutting out a core, measuring its volume, and measuring its mass after oven-drying at 105°C to constant mass. All soil samples were air-dried to constant mass; forest floor samples were then ground in a Wiley mill to pass a 2-mm sieve, while mineral soil samples were sieved through a 2-mm sieve to separate coarse fragments. Soil pH was measured with a pH meter and glass plus reference electrodes using a 1:1 suspension in water for the mineral soil and a 1:5 suspension for forest floor material. Total C was determined using a Leco Induction Furnace (Bremner and Tabatabai 1971). Total N was determined by semimicrokjeldahl digestion followed by estimation of NH_4 using a Technicon Autoanalyzer (Anonymous 1976).

Mineralizable-N was determined by an anaerobic incubation procedure modified from Waring and Bremner (1964). Released NH_4 was determined colorimetrically using a Technicon Autoanalyzer.

Mineralizable-N was expressed as concentrations on a dry mass basis and, where applicable, on a mass per unit area basis. The mass per unit area calculation used bulk density corrected for coarse fragment content for both forest floor and mineral soil and the results represent mass per hectare in the forest floor and surface 30 cm of the mineral soil.

Actual evapotranspiration (E_t) and components of the annual water balance were calculated using a slight modification of the Energy-Soil Limited water balance model of Spittlehouse and Black (1981) and 30-year normals for precipitation and temperature (Anonymous 1982). This model is driven by solar radiation, temperature, and precipitation using soil rooting depth and texture data to calculate available water storage capacity. Growing-season water deficit (WD) was calculated as the sum of daily potential evapotranspiration (E_{max}) minus E_t for each day of the growing season (April-

September). E_t was calculated as monthly totals during the growing season and as a growing season total.

Homogeneity of variance in vegetation cover and nutrient data was tested using Bartlett's procedure (Zar 1974). One-way analysis of variance (ANOVA) and T-tests (Zar 1974) were conducted to detect differences between vegetation units and site index, salal cover, foliar nutrients, soil chemical properties, and components of the annual water balance. Multiple comparisons were carried out on sample means using Scheffe's allowances (Zar 1974). Simple and multiple regression analyses were employed to examine relationships between site index, salal cover, vegetation units, and soil moisture and nutrient regimes (Chatterjee and Price 1977).

Results and Discussion

Plant Community Classification and Delineation of Biologically-equivalent Sites with High and Low Salal Cover

All the sample plots were classified into a hierarchy of vegetation units (associations and subassociations) representing early stages of secondary succession on different sites. For two of the three plant associations, two subassociations were delineated, making a total of five basic vegetation units (one plant associations and four subassociations) (Table 1). The associations and subassociations were delineated according to the floristic differences between the groups of plots (diagnostic combinations of species) which are summarized in Table 2. These vegetation units were named by the generic names of diagnostic or dominant understory species, as Douglas-fir was the dominant tree species in all units. The specific names were used to prevent ambiguities.

TABLE 1. The vegetation units distinguished in the study plots.

Plant association
Plant subassociation
<i>Gaultheria</i> — <i>Mahonia</i>
<i>Gaultheria</i> — <i>Mahonia</i> — <i>Polytrichum (juniperinum)</i> (1) ¹
<i>Gaultheria</i> — <i>Mahonia</i> — <i>Rhytidadelphus</i> (2)
<i>Mahonia</i> — <i>Kindbergia</i> (3)
<i>Polystichum</i> — <i>Mycelis</i>
<i>Polystichum</i> — <i>Mycelis</i> — <i>Mahonia</i> (4)
<i>Polystichum</i> — <i>Mycelis</i> — <i>Rubus (spectabilis)</i> (5)

¹A numerical symbol for a vegetation unit.

TABLE 2. Diagnostic combination of species for the plant associations (a.) and subassociations (sa.) distinguished in the study plots.

Number of plots		13	26	26	30	6	
Vegetation units and species	Diagnostic value ¹	Presence class ² and mean species significance ³					
<i>Gaultheria—Mahonia a.</i>							
<i>Gaultheria shallon</i>	(dd)	V 9	V 8	V 5	IV 4	I 1	
<i>Pinus monticola</i>	(d)	III 1	II 1	I +	I +	I 1	
<i>Rosa gymnocarpa</i>	(d)	III 1	III 1	I +	I +		
<i>Gaultheria—Mahonia—Polytrichum (juniperinum) sa.</i>							
<i>Polytrichum juniperinum</i>	(d)	III 1	I +	I +	I +	I +	
<i>Gaultheria—Mahonia—Rhytidiadelphus sa.</i>							
<i>Achlys triphylla</i>	(d)	II +	IV 4	IV 3	V 4	III 4	
<i>Rhytidiadelphus loreus</i>	(d)	I +	III 1	II +	III 1	II +	
<i>Mahonia—Kindbergia a.</i>							
<i>Polystichum—Mycelis a.</i>							
<i>Galium triflorum</i>	(d)	I +	I +	II +	IV 1	V 2	
<i>Polystichum—Mycelis—Mahonia sa.</i>							
<i>Achlys triphylla</i>	(d,c)	II +	IV 4	IV 3	V 4	III 4	
<i>Gaultheria shallon</i>	(d)	V 9	V 8	V 5	IV 4	I 1	
<i>Hylocomium splendens</i>	(d)	III 1	III 2	IV 2	IV 4	II +	
<i>Mahonia nervosa</i>	(d)	V 3	V 3	IV 4	IV 3	I 1	
<i>Rubus ursinus</i>	(d,c)	V 1	V 2	V 2	V 2	III 1	
<i>Polystichum—Mycelis—Rubus (spectabilis) sa.</i>							
<i>Athyrium filix-femina</i>	(d,c)		I +	I +	I +	V 4	
<i>Bromus vulgaris</i>	(d)	II +	II +	II +	II 1	IV 2	
<i>Dicentra formosa</i>	(d)					III 2	
<i>Gymnocarpium dryopteris</i>	(d)			I +	I +	IV 4	
<i>Petasites palmatus</i>	(d)					III 2	
<i>Rubus spectabilis</i>	(d,cd)	I +	I +	III 2	III 3	V 6	
<i>Sambucus racemosa</i>	(d)			I +	I +	IV 3	

¹Species diagnostic values: d—differential, dd—dominant differential, cd—constant dominant, c—constant (Pojar *et al.* 1987).²Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81-100.³Species significance class midpoint percent cover and range: + = 0.2 (0.1-0.3), 1 = 0.7 (0.4-1.0), 2 = 1.6 (1.1-2.1), 3 = 3.6 (2.2-5.0), 4 = 7.5 (5.1-10.0), 5 = 15.0 (10.1-20.0), 6 = 26.5 (20.1-33.0), 7 = 41.5 (33.1-50.0), 8 = 60.0 (50.1-70.0), 9 = 85.0 (70.1-100).

In order to examine the possible effect of salal on the stand and soil nutrient status and site index, it was necessary to consider only a group of plots with the same climatic, soil moisture, and soil nutrient regimes in order to eliminate variation due to non-plant influences on tree growth.

Based on a comparison of the site characteristics for each of the vegetation units (Table 3) and an assessment of where salal was most abun-

dant (in the *Gaultheria—Mahonia* association), it was decided to use plots from the *Gaultheria—Mahonia—Rhytidiadelphus* and *Mahonia—Kindbergia* units. These two vegetation units have similar soil properties as indicated by the data in Table 4. T-tests indicated that the only significant differences between the two units ($p < 0.05$) were in forest floor pH and total N. The quantitative soil parameters given in Table 4

TABLE 3. Average values of selected site characteristics of the distinguished vegetation units.

Vegetation unit	1	2	3	4	5
Number of plots	13	26	26	30	6
Biogeoclimatic unit ¹	-----CWHxm - dm-----				
Elevation (m)	270	230	250	230	210
Slope gradient (%)	16	17	16	19	8
Actual SMR ²	VD	MD-SD	MD-F	SD-F	M
Actual SNR ³	VP-P	VP-M	VP-M	P-R	R-VR
Humus form ⁴	MR-MD	MR-MD	MR-MD	MR-MD	MD
Forest floor depth (cm)	3	4	3	4	4
Soil particle size ⁵	S-L	S-L	S-L	S-L	L
Coarse fragments (%)	58	56	57	44	21
Rooting depth (cm)	60	60	60	70	90
Ground cover (%)					
—forest floor	75	82	69	70	82
—decaying wood	13	11	18	22	7
—mineral soil	3	<1	3	3	10
—coarse fragments	9	6	10	5	<1
Site index—mean	21	28	28	33	34
(m/50 yrs)—std. dev.	2.3	3.3	3.5	2.3	2.9

¹CWHxm—Very Dry Maritime CWH subzone, CWHdm—Dry Maritime CWH subzone.

²SMR (soil moisture regime): VD—very dry, MD—moderately dry, SD—slightly dry, F—fresh, M—moist.

³SNR (soil nutrient regime): VP—very poor, P—poor, M—medium, R—rich, VR—very rich.

⁴MR—Mor, MD—Moder.

⁵L—loamy, S—sandy.

TABLE 4. Means and standard deviations (in parentheses) of some physical and chemical characteristics of the soils in the *Gaultheria*—*Mahonia*—*Rhytidiadelphus* and *Mahonia*—*Kindbergia* vegetation units.

Vegetation unit	<i>Gaultheria</i> — <i>Mahonia</i> — <i>Rhytidiadelphus</i>	<i>Mahonia</i> — <i>Kindbergia</i>
Number of plots	10	8
Actual evapotranspiration (mm/year)	236 (23)	221 (27)
Water deficit (mm/year)	43 (27)	65 (48)
Forest floor thickness (cm)	4.0 (2.4)	3.6 (2.2)
Forest floor pH	4.8 (0.3)	5.1 (0.2)
Forest floor C (%)	37.8 (4.0)	39.7 (3.8)
Forest floor N (%)	1.04 (0.12)	0.89 (0.11)
Forest floor C/N ratio	36 (5)	45 (4)
Forest floor mineralizable-N (ppm)	390 (138)	228 (188)
Mineral soil mineralizable-N (kg/ha)	14.1 (5.7)	16.5 (4.1)

are those which have been found to be the most important for characterizing soil moisture (Major 1963; Giles 1983; Carter and Klinka pers. comm.) and soil nutrient regimes (Carter and Klinka pers. comm.; Kabzems and Klinka 1987a,b; Courtin *et al.* in press). Accordingly 15 plots could be selected from each of the two vegetation units such that each plot had the same regional climate (the same biogeoclimatic subzone—CWHxm) and the same soil moisture (moderately dry) and nutrient (poor) regime. All these 30 plots are considered to have similar site quality and to develop in the climax *Pseudotsuga—Gaultheria—Mahonia* plant association (Kojima and Krajina 1975).

The major difference between the two sets of selected plots is in the cover of salal which ranged from a mean of 60 percent (5 to 100 percent range) for the 15 plots belonging to the *Gaultheria—Mahonia—Rhytidadelphus* unit to a mean of 15 percent (0 to 33 percent range) for the 15 plots belonging to the *Mahonia—Kendallia* unit. This difference in salal cover was significant at $p < 0.01$. Data from these 30 plots were then used to test two hypotheses; firstly that salal competes successfully against Douglas-fir for both available soil water and nutrients; and secondly, that there is a strong relationship between the cover of salal and Douglas-fir site index on these moderately dry, nutrient-poor sites.

Reasons for the difference in salal cover between the 30 biologically-equivalent plots cannot be determined with certainty. There is no information on understory vegetation in the original old-growth stands prior to their harvest. However, high salal cover (absolutely dominating) on very to moderately dry and nutrient-poor sites in the drier maritime CWH subzones has been documented and is generally associated with the presence of acid forest floors (Mor humus forms) and the absence of dense tree or high-brush layers (Spilsbury and Smith 1947; McMinn 1957; Mueller-Dombois 1959; Orloci 1961, 1964; Krajina 1969; Kojima and Krajina 1975; Beese 1981; Klinka and Krajina 1986).

The forest floor in old-growth stands of the *Pseudotsuga—Gaultheria—Mahonia* association was reported to have a mean of 4.4 cm and 3 to 12 cm range in thickness (compared to the mean of 3.5 cm and 1 to 12 cm range in this study), with a mean pH of 4.8 (range 4.2 to 5.5), and a mean C/N ratio of 37 (range 18 to 62) (Kojima

and Krajina 1975). These data are characteristic of less-acidic Mors and Mormoders (Klinka *et al.* 1981, Klinka and Nuszdorfer 1988). In contrast, salal-dominated sites that feature forest growth stagnation generally have thick (usually over 10 cm) forest floors largely composed of residues which are resistant to decomposition and/or decaying coniferous wood (lignic and residuic Mors), are strongly acid (mean pH 3.8, range 3.1 to 4.3), and have a high C/N ratio (mean 54, range 34 to 79) (Klinka and Nuszdorfer 1988).

On nutrient-rich to -very rich sites with Moder or Mull humus forms, salal may be present but it is restricted to acid organic microsites, such as decaying coniferous wood (Kojima and Krajina 1975, Klinka and Krajina 1986). It is probable that high salal cover sites were not burned or burned only lightly with sufficient forest floor materials left for resprouting of rhizomes and re-establishment of salal during the treeless stages of succession, and that the understory light conditions during the life of the stands have provided for salal growth under the tree canopy (Long and Turner 1975, Stanek *et al.* 1979). Low salal cover sites might have a similar history of disturbance but the presence of dense tree or shrub layers restricted the development of semi-tolerant salal in the understory. Forest floor materials may also have been destroyed by fire with no suitable substrate left for salal establishment. Observations indicate that salal is absent in immature Douglas-fir stands with a dense western redcedar understory, probably due to poor light conditions and/or the effect of western redcedar on forest floor quality, or under the canopy of scattered bigleaf maple (*Acer macrophyllum* Pursh), likely due to the presence of Mull humus forms.

Relations Between Salal Cover, Foliar Nutrients, and Site Index on Biologically-equivalent Sites

In the absence of significant differences in soil moisture and soil nutrient characteristics, it might be expected that there were no significant differences between high and low salal cover sites in the foliar nutrient levels in the Douglas-fir trees. This was, in fact, found when the foliar nutrient levels were compared ($p < 0.05$; Table 5). There were also no significant differences ($p < 0.05$) between the sites in Douglas-fir site index. When the results of all comparisons between the high and low salal cover sites are

TABLE 5. Mean foliar nutrient concentrations (dry-mass basis) of the Douglas-fir trees in the 15 biologically-equivalent plots in each of the *Gaultheria*—*Mahonia*—*Rhytidadelphus* and *Mahonia*—*Kindbergia* vegetation units. Standard deviations are given in parenthesis.

Nutrient element	<i>Gaultheria</i> — <i>Mahonia</i> — <i>Rhytidadelphus</i>	<i>Mahonia</i> — <i>Kindbergia</i>
Mass of 100 needles (mg)	472 (79)	492 (71)
Nitrogen (%)	1.17 (0.078)	1.17 (0.116)
Phosphorus (%)	0.209 (0.036)	0.199 (0.042)
Calcium (%)	0.397 (0.067)	0.414 (0.047)
Magnesium (%)	0.130 (0.022)	0.129 (0.014)
Potassium (%)	0.689 (0.080)	0.687 (0.070)
Sulphur (%)	0.131 (0.023)	0.128 (0.018)
Sulphate-sulphur (ppm)	325 (135)	312 (133)
Copper (ppm)	3.9 (0.52)	3.7 (0.59)
Zinc (ppm)	19.4 (3.87)	20.5 (2.47)
Manganese (ppm)	547 (327)	499 (257)
Boron (ppm)	19.5 (8.82)	21.9 (5.87)
Active-iron (ppm)	42 (11.5)	39 (12.9)

taken into account, it appears that, on apparently biologically-equivalent sites, high salal cover did not adversely affect the height growth of Douglas-fir in the ecosystems studied.

Stanek *et al.* (1979) reported increases in the biomass and nitrogen content of salal following thinning and nitrogen fertilization in immature stands on sites similar to those used in the present study (i.e., the *Gaultheria*—*Mahonia* association), but concluded, in agreement with other workers (Gessel *et al.* 1973, Björkman *et al.* 1967, Mead and Pritchett 1975), that the amount of nitrogen tied up by salal was relatively small and not likely to be critical for tree growth except on nutrient-very poor sites (Miller *et al.* 1976).

Brix and Mitchell (1986), in a study of the same ecosystems examined by Stanek *et al.* (1979), suggested that removal of the salal understory in thinned and fertilized stands did not affect the soil or predawn shoot water potential. However, the studies of Black and coworkers (Spittlehouse and Black 1981, Tan *et al.* 1977, Kelliher and Black 1986, Price *et al.* 1986) showed that the salal understory can account for a large fraction of stand water consumption, especially toward the latter part of the dry period in late July and early August. Because Douglas-fir develops terminal buds approximately at the onset of the dry period, subsequent soil water deficits, possibly exacerbated by salal water consumption, are not likely to have a significant influence in height growth, vis-a-vis site index. This could explain the failure of this study to find significant differences in Douglas-fir site index between the high and low salal cover sites. The studies by Black and coworkers also showed that the removal of salal slightly improved basal area increment by 0.5 to 2.3 percent.

Relations Between Site Index, Salal Cover, Vegetation Units, and Site Variables

The frequency and mean cover of salal decreased from 100 percent and 73 percent in the *Gaultheria*—*Mahonia*—*Polytrichum* (*juniperinum*) unit to 16 percent and 0.6 percent in the *Polystichum*—*Mycelis*—*Rubus* (*spectabilis*) unit, respectively. If salal exerted a profound influence on forest productivity, then a reasonable relationship might be expected between its cover and stand growth performance. For this purpose, the relationship between site index and salal cover (estimated as midpoint percent cover of the species significance scale) was examined across all 101 study sites. A simple linear regression of SI (m/50 yr) as a function of salal cover produced the following equation:

$$[1] \text{ SI} = 32.44 - 0.71 (\text{midpoint percent salal cover}) \\ R^2 = 0.23 \quad F = 30.17 \quad SE = 4.45 \text{ m}$$

Although significant ($p < 0.01$), the equation explained only a small amount of the variation in Douglas-fir site index across a wide range of sites. This regression appears to reflect the relationship between salal and humus form quality, in that salal cover generally decreased as the humus form changed from Mor to Moder or Mull. This humus form change occurred progressively

from vegetation unit 1 through 5 (Table 2). The respective means of the midpoint percent cover values for salal are 73, 60, 15, 7.5, and 0.6 percent, in vegetation units 1 through 5, respectively.

Regressions of site index (m/50 yr) on component scores extracted from the first two PCA axes based on all understory diagnostic species and vegetation units were also examined. These resulted in the following equations:

$$[2] \text{ SI} = 30.55 + 0.70 (\text{PCA1}) + 0.32 (\text{PCA2})$$

$$R^2 = 0.36 \quad F = 28.00 \quad SE = 4.15 \text{ m}$$

where PCA1 and PCA2 refer to scores for axis 1 and 2, respectively; and,

$$[3] \text{ SI} = 34.3 - 13.2 \text{ U1} - 5.8 \text{ U2} - 6.45 \text{ U3} - 0.87 \text{ U4}$$

$$R^2 = 0.67 \quad F = 49.70 \quad SE = 2.94 \text{ m}$$

where U1-U4 are dummy variables with unit value, for the *Gaultheria*—*Mahonia*—*Polystichum* (*juniperinum*), *Gaultheria*—*Mahonia*—*Rhytidadelphus*, *Mahonia*—*Kindbergia*, and *Polystichum*—*Mycelis*—*Mahonia* units, respectively.

Site index for units 1 through 4 is equal to the intercept term plus the partial coefficient of the corresponding dummy variable, while the site index for unit 5 [*Polystichum*—*Mycelis*—*Rubus* (*spectabilis*)] is equal to the intercept term (34.3) since the dummy variable for this variable is always equal to zero. Results of ANOVA showed that the variances for site index among vegetation units were homogeneous ($p < 0.05$) and that site index differed significantly ($p < 0.01$; $F = 44.25$) among the vegetation units. The mean site indices of units 2 and 3 and 4 and 5 were not significantly different ($p > 0.05$).

Equation [1] suggests that there is poor correlation between salal cover and Douglas-fir site index across all study plots. However, a significant improvement resulted when the regression was based on either the scores for the first and second axis of the PCA (based on diagnostic species) or the vegetation units rather than salal cover.

Climatic, soil moisture, and soil nutrient regimes are used in the biogeoclimatic ecosystem classification to differentiate among biologically-equivalent sites (Pojar *et al.* 1987). In order to determine whether these variables have a stronger relationship to productivity than the vegetation characteristics of a site, the relationship between site index (m/50 yr), soil moisture

regime (SMR) and soil nutrient regime (SNR) was examined. Climatic regime (biogeoclimatic unit) was not included as all study ecosystems were distributed within the very dry maritime cool mesothermal climate (the CWHxm subzone). Multiple linear regression produced the following equation:

$$[4] \text{ SI} = 35.5 - 7.50 \text{ VD} - 1.72 \text{ MD} + 3.33 \text{ F} - 9.10 \text{ VP} - 5.03 \text{ M} - 1.75 \text{ R}$$

$$R^2 = 0.86 \quad F = 68.62 \quad SE = 1.99 \text{ m}$$

where VD (very dry), MD (moderately dry), SD (slightly dry), and F (fresh) are dummy variables, with unit value, designating SMRs; while VP (very poor), P (poor), M (medium), and R (rich) are dummy variables, with unit value, designating SNRs.

Thus, variables representing the SMRs and SNRs were better predictors of site index than vegetation variables. This is to be expected because understory vegetation often has a less pronounced effect on site quality, than humus form and mineral soil fertility factors. Furthermore, the understory vegetation which grows up after a timber harvesting operation may depend more on factors such as site disturbance, stand structural characteristics, time, and chance. This suggests that SMR and SNR—site factors that directly affect plant growth—offer a simple means of characterizing site quality and explaining forest productivity. Although understory vegetation may provide a good indication of site quality and can influence forest floor formation and decomposition rate through above- and below-ground litter production, such vegetation is usually a symptom, rather than a controlling factor, of site quality.

Salal, and other ericaceous plants are known to thrive in, and, hence, indicate the presence of Mor humus forms (e.g., Ellenberg 1974, Klinka *et al.* in press). However, Mor humus forms are often found in the absence of ericaceous plants and, due to their relatively wide ecological amplitude, ericaceous plants are actually found over a wide range of soil nutrient regimes—from nutrient-very poor (characterized by lignic and residuic Mors) to nutrient-poor (characterized by orthic Mors) to nutrient-medium (characterized by friable Mors or Mormoders) (Klinka *et al.* 1981, in press).

Conclusions

There were few significant differences in soil and foliar chemical properties between the high and low salal cover ecosystems having similar climatic, soil moisture, and soil nutrient regimes. Regression analyses showed poor relationships between Douglas-fir site index and salal cover. Much better relationships were obtained using variables representing vegetation units or SMRs and SNRs. These results imply that salal may not significantly influence height growth in immature Douglas-fir stands growing on moderately dry and nutrient-poor sites within very dry, cool

mesothermal climates. A different sampling design and further experimental testing would be required to prove this conclusively.

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Home Ranges of Elk in an Arid Environment

Abstract

Home ranges of elk (*Cervus elaphus nelsoni*) inhabiting montane and coastal forests have been previously documented, but few estimates have been reported for elk occupying non-forested habitats. We analyzed the home ranges of elk inhabiting the treeless shrub-steppe of Washington using 782 relocations of eight radio-collared individuals during 1983 and 1984. Annual minimum convex polygon estimates averaged 161.4 km² for female elk and 163.1 km² for male elk. Annual ninety-five percent confidence ellipses averaged 305.1 km² for female elk and 284.6 km² for male elk. Seasonal home ranges of female elk decreased significantly each season from spring through fall. Large home ranges of elk in the shrub-steppe relative to elk in more mesic environments are hypothesized to be a strategy to compensate for low forage density in the arid shrub-steppe. These elk maintained large home ranges yet were reproductively successful, indicating that large home ranges can be an effective strategy for large herbivores faced with low food densities. We hypothesize that the success of these elk was mediated by the quantity rather than the quality of foraging areas in a prairie-like environment. Home range shapes appeared to be related to the availability of disturbance-free areas. A review of the literature suggested annual precipitation may be a relatively good predictor of home range sizes for elk.

Introduction

Numerous home range estimates for North American elk have been published (Craighead *et al.* 1973, Waldrip and Shaw 1979, Hershey and Leege 1982, Jenkins and Starkey 1982, Irwin and Peek 1983, Edge *et al.* 1985), but these estimates have almost universally concerned elk inhabiting mesic montane or coastal forests. No data are available for elk inhabiting non-forested environments. In this paper, we report on home ranges of Rocky Mountain elk (*C. e. nelsoni*) inhabiting the arid, treeless shrub-steppe of Washington.

Study Area

The study was conducted on the Arid Lands Ecology (ALE) Reserve, a 330 km² ecological reserve, associated with the U.S. Department of Energy's Hanford Site in southcentral Washington (46°30'N, 119°40'W). The ALE Reserve is bordered on the west and south by private rangeland and agricultural land, and on the north and east by paved public highways. Public access to the ALE Reserve is prohibited. The site is surrounded by a 110-cm barbed wire fence that did not restrict elk movements. The site is patrolled weekly by fixed-wing aircraft. The Hanford

Site is a federal nuclear materials production and processing area. However, facilities and personnel associated with these processes are limited to areas beyond the ALE Reserve boundaries.

Local vegetation of the ALE Reserve is climax-dominated by big sagebrush (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*), Sandberg bluegrass (*Poa sandbergii*), or cheatgrass brome (*Bromus tectorum*) (McCorquodale *et al.* 1986). Historical rangefires have removed the sagebrush canopy from approximately 90 percent of the reserve. Limited riparian vegetation occurs at several small springs in the western part of the reserve.

The physiography of the site has been described in detail by McCorquodale *et al.* (1986). Elevations range from 150 to 1,090 m. The arid site receives less than 16 cm of precipitation annually.

The elk population of the ALE Reserve was established by natural colonization during the winter of 1972. The population increased from 27 to 55 elk during this study ($r = 0.36$), due entirely to reproduction (McCorquodale *et al.* 1988).

Methods

Eight adult (4 F: 4M) radio-collared elk were relocated 782 times by ground or aerial tracking (92 percent of locations verified visually)

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between January 1983 and September 1984. Female elk were relocated three times weekly (minimum) from April through September and twice monthly during winter. Male elk were relocated twice weekly (minimum) from April through September and twice monthly during winter. Thirty-seven percent of locations were obtained from 0500 to 0900 hours, 38 percent from 0900 to 1300, and 22 percent from 1300 to 1700. We were careful not to disturb collared elk while radio-tracking, and we noted few extraneous disturbances to elk during this study. Elk locations were referenced to the nearest 100 m of the Universal Transverse Mercator System. Elk were not located more than once daily in order to reduce autocorrelation of relocations (Swihart and Slade 1985).

Annual and seasonal home range estimates were obtained by the minimum convex polygon method (MCP) (Odum and Kuenzler 1955) and by 95 percent bivariate normal confidence ellipses (CE) (Jennrich and Turner 1969). These methods were used to calculate most published estimates of elk home ranges and we selected them to enhance the comparability of our estimates.

Seasonal home ranges were calculated for spring (April-May), summer (June-August), and fall (September-October) by year. Winter home ranges were not reported due to small sample sizes; winter data were included in annual estimates. Annual estimates were calculated for 1983 and 1984.

Minimum daily mobility within the home range for female elk was indexed by calculating

the distance between consecutive day locations. These data were analyzed on the same seasonal basis as the home range data.

The null hypothesis that annual and intra-seasonal home ranges did not vary between years was tested using paired t-tests and estimates from three female elk monitored both years. The hypothesis that inter-seasonal home ranges did not vary was tested with a Kruskal-Wallis test and nonparametric multiple comparisons (Zar 1974: 156-157). Statistical tests were not conducted using data from male elk due to the small number of males marked (2 each year).

Data from this study and several others were used to test the hypothesis that precipitation influences elk annual home range size. The relationship was evaluated using simple least squares linear regression after precipitation was transformed ($1/x$ of precipitation) to improve the linearity of the relationship. The hypothesis was tested using a t-test for slope of the regression ($H_0: b = 0$). We limited the regression to polygon (minimum convex or minimum area) estimates since home range estimates are influenced by estimation method (Anderson 1982) and because more polygon estimates were available in the literature.

Results

Sizes of annual home ranges for female elk were not significantly different between years [$P > 0.20$ (MCP), $P > 0.50$ (CE)], so annual estimates were pooled (Table 1). No significant differences were detected between spring ranges ($P > 0.50$ both methods), summer ranges [$P > 0.20$ (MCP),

TABLE 1. Home range estimates (km²) for elk on the ALE Reserve, Washington ($\bar{X} \pm 1$ SE)

	Female Elk				Male Elk			
	N	Loc ^a	MCP ^b	CE ^c	N	Loc ^a	MCP	CE
Annual	7	85	161.4 $\pm$ 8.5	305.1 $\pm$ 23.3	3	51	163.1 $\pm$ 17.4	284.6 $\pm$ 47.2
Spring	7	20	125.3 $\pm$ 9.2	368.1 $\pm$ 43.0 ^d	2	12	60.7 $\pm$ 7.3	226.8 $\pm$ 15.5
Summer	7	44	95.2 $\pm$ 6.1	190.5 $\pm$ 8.8	3	25	117.7 $\pm$ 26.6	277.2 $\pm$ 99.8
Fall	7	12	25.3 $\pm$ 2.4	83.7 $\pm$ 11.7	3	11	25.0 $\pm$ 2.4	87.4 $\pm$ 23.7

^aMean number of locations per individual.

^bMinimum Convex Polygon.

^cConfidence Ellipse.

^dSpring CE larger than annual CE due to the greater effect of outliers when location number is small.

$P > 0.10$ (CE)], or fall ranges [$P > 0.20$ (MCP), $P > 0.10$ (CE)] between years, so data from the two years were pooled for inter-seasonal comparisons. Spring home ranges were significantly larger than both summer and fall ranges ($P < 0.01$ both methods), and summer ranges were significantly larger than fall ranges ($P < 0.01$ both methods).

Individual home range polygons were similar since the population consisted of one major social group and since there was a high degree of relatedness between individuals (McCorquodale *et al.* 1988). The majority of unmarked elk on the reserve were continually associated with the marked elk except during subgrouping periods (spring, parturition, and rut), suggesting our marked elk were representative of the population. Home ranges generally conformed to the shape of the reserve (Figure 1). Elk were never located on other parts of the Hanford Site, but some did occasionally move onto adjacent private rangeland to the west. Male elk were more frequently relocated beyond the reserve's boundaries, but one marked female spent a considerable part of June and July 1984 off the reserve before returning during August. Elk located off the reserve eventually returned in every case.

Distances between consecutive day locations were greatest in spring (3523.0 ± 586.3 m [1 SE], $n = 49$), smallest in summer (2185.7 ± 155.3 m, $n = 173$), and intermediate in fall (3010.7 ± 358.9 m, $n = 39$). Movements were more variable in spring than during the remainder of the year.

Home range data from several elk populations suggested that annual precipitation influences elk home range sizes, with home ranges decreasing with increasing precipitation ($t = 13.6$, $df = 5$, $P = 0.0001$) (Figure 2). The relationship is also significant without our data ($t = 3.7$, $df = 4$, $P = 0.02$). Including our data, $r^2 = 0.97$; excluding our data, $r^2 = 0.77$.

Discussion

Annual and seasonal home ranges of elk on the ALE Reserve were approximately 3-10 times larger than those reported in the literature for elk in forested regions (Craighead *et al.* 1973, Franklin and Lieb 1979, Waldrip and Shaw 1979, Jenkins and Starkey 1982, Irwin and Peek 1983, Edge *et al.* 1985), (Martinka 1969, Craighead *et al.* 1973, Schoen 1977, Bowyer 1981). Distances between

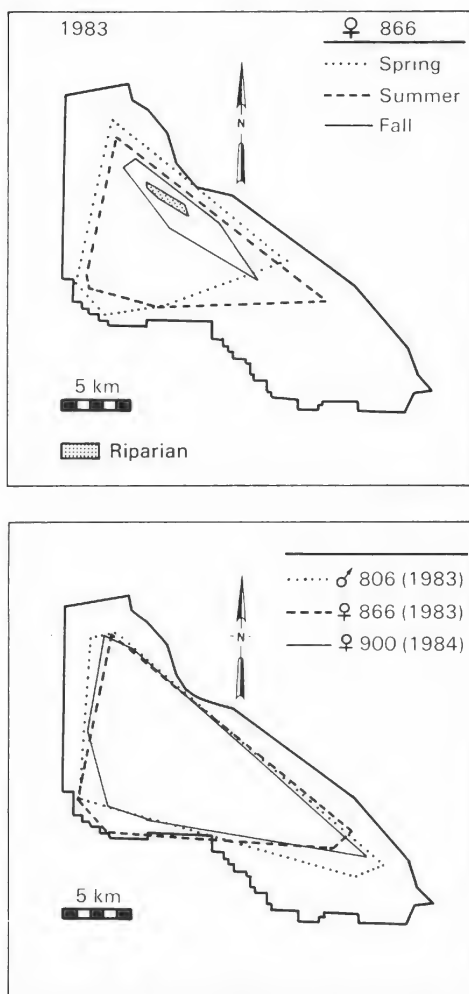


Figure 1. Annual and seasonal home range polygons of radio-collared elk on the Arid Lands Ecology Reserve, Washington, 1983-84.

consecutive day locations for the ALE population were 2-5 times greater than the same distances measured for elk populations inhabiting forested habitats (Harper 1971, Craighead *et al.* 1973, Hanley 1980, Bowyer 1981).

Estimates of home range size tend to inflate as relocations are added until an asymptote is reached. Probability ellipse estimates tend to be less sensitive to number of relocations than are polygon estimates (Anderson 1982, Eberhardt *et*

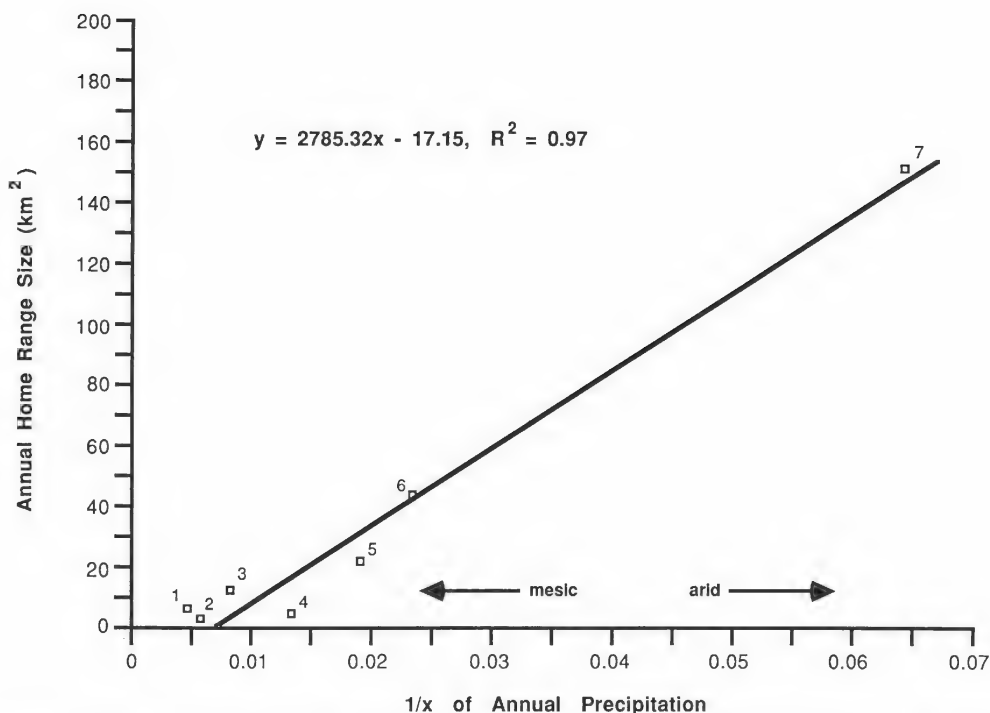


Figure 2. Linear regression of annual home range size for elk and annual precipitation (transformed $1/x$, where x = cm). Data are from: 1. Janz and Becker (1986); 2. Franklin and Lieb (1979); 3. Irwin and Peek (1983); 4. Waldrup and Shaw (1979); 5. Craighead *et al.* (1973); 6. Edge *et al.* (1985); 7. this study.

al. 1984). Our fall home range estimates may be conservative due to the small number of relocations; however, our mean number of relocations per individual during fall represents knowledge of their location on 20 percent of all possible days within the season. Our spring sample of relocations was small relative to summer, but additional relocations in spring would only have inflated the home range estimates, thus increasing the significance of differences between spring and summer ranges.

Home range size within a species typically increases with decreasing food density (McNab 1963). Primary production on the ALE Reserve is approximately 1/5 that of temperate forests (Whittaker and Likens 1973, Rickard 1985). Variation in home range size amongst elk inhabiting a range of environments from very mesic to arid appears to be strongly influenced by precipitation which largely determines primary production (Figure 2). A general trend towards increasing home

range size with increasing aridity has been noted for a variety of mammals by Harestad and Bunnell (1979). Home ranges of mule deer (*Odocoileus hemionus*) on the Hanford Site also tended to be larger than those of deer studied in more mesic habitats (Eberhardt *et al.* 1984).

An animal's home range may reflect social factors as well as food density. Thus, as demonstrated by McCullough (1969), Varland *et al.* (1978), Franklin and Lieb (1979), and Edge *et al.* (1986), the home ranges of distinct social groups of elk are often disjunct in areas supporting multiple social groups. Since the ALE Reserve elk exclusively occupied their range, their home ranges may have lacked social constraints operating in areas supporting multiple social groups. In the shrub-steppe there also tend to be few natural geographic barriers such as drainage divides which might constrain elk movements.

Female elk home ranges and daily movements on the ALE Reserve were largest during spring

when plants were growing, while movements and home ranges appeared to decrease in summer. We hypothesize that this reflects increasing constraints on elk movements with the onset of summer drought. Summer and fall ranges of lactating elk became increasingly smaller areas centered around permanent water sources and riparian habitat (Figure 1) (McCorquodale *et al.* 1986). As grasses and forbs dessicated by early fall, succulent forage was available only in riparian habitats. Elk also showed a preference for bedding in sagebrush-dominated habitats during the heat of summer, and these areas were limited to 10 percent of the ALE Reserve (McCorquodale *et al.* 1986). Although food density was low in the shrub-steppe and elk home ranges large, these elk were reproductively quite successful (McCorquodale *et al.* 1988). This suggests that a large home range can be an effective herbivore strategy when food densities are low. We hypothesize that these elk may be successful on the basis of the quantity rather than the quality of foraging areas. In the shrub-steppe, there may be few areas that compare with mesic forest meadows in terms of forage production, but nearly the entire landscape produces forage in the absence of an overstory canopy. Locally, food densities were low, but potential foraging areas were extensive in the prairie-like habitat of the ALE Reserve.

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- While home range size appeared to be largely determined by forage production, home range shape and orientation appeared to be strongly influenced by the availability of disturbance-free areas. In the absence of extensive security cover, elk largely confined their activities to the secluded ALE Reserve, perhaps compensating for a lack of security cover by locating their home ranges within a large disturbance-free zone. Elk did not use other parts of the Hanford Site where human activity associated with energy technology was common. Elk were also reluctant to use agricultural lands bordering the reserve, at least during daylight hours; however, elk did occasionally use adjacent private rangeland where human activity was not common.
- These results suggest that although the shrub-steppe biome is capable of supporting viable elk populations, relatively large, disturbance-free areas of contiguous habitat may be required for successful colonization.

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Detecting Female Mountain Lions with Kittens³

Abstract

Mountain lion (*Felis concolor*) hunting programs typically include prohibitions against killing females with kittens. It may be difficult, however, for hunters to differentiate females with kittens from other mountain lions because young are often not with their mothers. We investigated the association between female mountain lions and their kittens in southern Utah, using radio-telemetry locations and examinations of tracks of females known to have kittens. Females were with their kittens on 67 percent of the occasions radio-collared families were located, but kitten tracks were found with their mother's only 25 percent of the time. Because tracks are the sign most available to hunters, 75 percent of females with kittens would not be recognized. The effectiveness of regulations designed to protect female mountain lions with young is limited by the ability of hunters to identify these individuals.

Introduction

Most states and provinces with viable mountain lion populations allow sport-hunting of the species. Regulations governing these hunts often include prohibitions against killing kittens and females accompanied by kittens. The effectiveness of such regulations, however, requires that the hunter be able to identify protected individuals. Kittens may be recognizable to a hunter because of their size and spots, while a female with dependent young may be difficult to identify. Kittens can survive on their own at six months (Shaw 1980, Hemker *et al.* 1984), but will likely die if abandoned at an earlier age. The most common method of hunting mountain lions is to locate a track, generally in the snow, and release trained dogs to trail and tree the animal. Although nursing females can be recognized by worn or matted hair around their nipples, such sign may be present for only a short period. Eaton and Velandier (1977) noted that three captive mountain lion kittens stopped nursing at 60 days. The short duration of such sign and the difficulty of seeing matted hair on a mountain lion in a tree limits the utility of this approach in identifying females with kittens. Relying on tracks to identify females with kittens may be similarly limited because kittens do not always travel with their mother (Hemker *et al.* 1984). This paper

examines the frequency with which kittens are found with their mother as one measure of the ability of hunters to determine whether a female mountain lion has young.

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Study Area

The study area encompasses 4,500 km² of the Boulder, Escalante, and Canaan Mountains in southern Utah. Research efforts were concentrated in a core area of approximately 1,900 km². Elevation varies from 1,350 m on the Escalante River to 3,355 m on the Boulder Mountain. Precipitation comes mainly as snow in the winter and afternoon thunder storms during August and September. Average annual precipitation ranges between 18 cm at Escalante and 60 cm at higher elevations.

Most of Utah's major vegetation zones are represented on the study area. Below 1,800 m, sparse pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*) dominate the overstory; desert grass/shrub complexes dominate the understory. Bare sandstone ridges occur in the rougher terrain, and dense pinyon-juniper woodlands are interspersed with big sagebrush (*Artemisia tridentata*) flats in the less rugged areas between 1,800 m and 2,400 m. Ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*) dominate the zone between 2,400 m and 2,700 m. Above 2,700 m, small mountain lakes and sub-alpine meadows are surrounded by Engelmann spruce (*Picea engelmannii*) and white

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fir (*Abies concolor*) forests and stands of quaking aspen (*Populus tremuloides*).

Methods

Adult mountain lions were treed using trained dogs, immobilized with a ketamine hydrochloride and xylazine hydrochloride mixture, and fitted with radio-transmitter collars (Hemker *et al.* 1984). Kittens were located and captured by searching areas where adult females concentrated activities. Kittens were either fitted with drop-off collars similar to those described by Garcelon (1977) or recaptured periodically to enlarge their collars to accommodate growth; they also were fitted with progressively larger transmitters as they grew. Age of kittens was estimated based on tooth eruption (Ashman *et al.* 1983) and they were placed into one of three age-related classes (class 1: 0-6 months, class 2: 7-12 months, class 3: 13-18 months). Radio-collared mountain lions were located from an airplane or by triangulating from known locations on the ground during daylight hours.

We assumed that a hunter's ability to distinguish a female with kittens was directly related to the time a female was with her kittens, particularly the frequency with which they traveled with her. Same-day telemetry locations of females and their kittens and the frequency with which kitten tracks were found with their mother's tracks were used as measures of association. Tracks of radio-collared females were located by driving roads in a truck or snowmobile and riding trails and roads on horseback, all common methods employed by sport-hunters. Telemetry data were collected from 1979 to 1983. Track searches were conducted during 1982 and 1983.

Results

Radio-collared females and their radio-collared kittens were located on the same day 414 times. Class 1 kittens were with their mothers 63 percent of the times they were both located, class 2 kittens 69 percent, and class 3 kittens 65 percent (Table 1). Tracks of class 1 kittens were found with those of their mother's only 19 percent of the times their mother's tracks were encountered. Tracks of class 2 kittens were found with their mother's tracks 43 percent of the time (Table 1). Too few tracks of females with class 3 kittens were found to include in these analyses.

TABLE 1. Percent of time female mountain lions were radio-located with their kittens and percent of time female and kitten tracks found together.

Age of kittens (mo)	Telemetry locations			Tracks		
	Litters	N	%	Litters	N	%
0-6	2	109	63	4	75	19
7-12	4	222	69	2	28	43
13-18	5	83	65			

Discussion

Mountain lions are nocturnal/crepuscular (Ackerman 1982) and would more likely be with their young during daylight hours. Thus, our day-time telemetry data probably overestimated the proportion of time females spend with their young. Additionally, the probability of locating a female and her kittens on the same day was enhanced when they were together or close to one another. This bias is probably greater in data for class 2 and 3 kittens, because females tend to move greater distances as their kittens become older (Hemker *et al.* 1984).

The percent of time kitten tracks are found with their mother's tracks is a more direct measure of the probability of a hunter knowing whether a mountain lion has kittens. Only one of five times a hunter locates tracks of a female with class 1 kittens would it be obvious that she had kittens. The probability of detecting kittens more than doubles after the kittens are about six months of age, but is still less than 50 percent. Because a female's trail will eventually lead to her kittens, however, a hunter will occasionally be able to detect the presence of kittens before capturing the female. Unfortunately, the likelihood of dogs trailing a female to her kittens is greatest during the period that the female returns frequently to her kittens to nurse. Kittens of this age are often unable to escape and are susceptible to being caught and killed by the dogs (Roberson 1984:124).

Regulations that prohibit killing female mountain lions with young will always have limited effectiveness because hunters cannot easily recognize these females. Additional protection of females and their kittens may be provided by adjusting the timing of sport-hunting seasons. Generally, the older kittens are, the more easily

their mother will be recognized as having kittens, the better their chances of survival if orphaned,

and the less likely they will be caught and killed by dogs.

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Reproduction and Mortality of Great Gray Owls in Oregon

Abstract

We observed population characteristics of great gray owls (*Strix nebulosa*) in northeastern Oregon from 1982 to 1986 for information needed to manage this species. Of 64 nesting attempts, 77 percent of the pairs raised young. Mean brood size was 2.3 (SD = 0.87, range = 1-5). Annual probability of survival of adult nesting females and males was 0.84 (CL = 0.70-1.00) and 0.91 (CL = 0.78-1.00), respectively. Probabilities of young owls surviving their first 12, 18, and 24 months of life were 0.53 (CL = 0.44-0.75), 0.39 (CL = 0.24-0.65), and 0.31 (CL = 0.16-0.57), respectively. This baseline information on reproduction and survival is essential to the management of populations of great gray owls.

Introduction

Great gray owls are uncommon throughout their range in North America. They were even considered rare in the United States until recently (Winter 1986, Franklin 1987, Forsman and Bryan 1987). Little is known of this species, yet information on the population dynamics is essential for the effective management of this owl. If a management goal is to maintain a specified population density over time, information is needed on reproduction, mortality, age of breeding, and life expectancy. These population characteristics of the great gray owl are addressed in this paper.

Study Area

The study was conducted in four study areas (called Spring, Bowman, Sheep, and Thomason) in northeastern Oregon. The Spring study area (44 km²) was 17 km west of La Grande at 930-1140 m elevation. Cover types included conifer forest (63 percent of area), shallow-soiled grasslands (32 percent), and clearcuts (5 percent). Most of the forests in this area consisted of open, park-like stands dominated by ponderosa pine (*Pinus ponderosa*); 22 percent of this study area contained denser stands of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*).

Bowman (27 km²) was 50 km west of La Grande at 1380-1500 m elevation. Cover types included conifer forest (68 percent), shallow-soiled grasslands (20 percent), and clearcuts (12

percent). Dense stands of lodgepole pine or dense stands of grand fir (*Abies grandis*) and Douglas-fir with some western larch and ponderosa pine dominated the Bowman area.

Sheep (78 km²) was 37 km southwest of La Grande at 1290-1500 m elevation. Cover types included conifer forest (68 percent), clearcuts (12 percent), wet meadows along streams (12 percent), and shallow-soiled grasslands on ridges (8 percent). Ponderosa pine forests occurred on south-facing slopes, and lodgepole pine stands or mixed stands of Douglas-fir, western larch, and grand fir occurred on north-facing slopes.

Thomason (34 km²) was 47 km north of Enterprise at 1350-1470 m elevation. Cover types included coniferous forest (71 percent) and wet meadows (29 percent). Forest stands were lodgepole pine and ponderosa pine or mixed stands of Douglas-fir, western larch, and grand fir.

Methods

We located owls by hiking through the study areas after dark in February, March, or April (1982-1986), and imitating the territorial call of a male great gray owl every 0.1 km. Areas where owls responded were searched during the day to locate nests. After a nest was found, we visited it weekly, if possible, to determine nesting success and productivity. We recorded brood size either by climbing to the nest within a week of fledging or waiting until after the young left the nest.

We compared dates that females started incubating and dates that young left the nest among study areas and years using a two-way

¹Deceased.

analysis of variance and an LSD test for multiple comparisons. Sheep was not included in this analysis due to a small sample size. Nesting success was compared among study areas with a chi square analysis. Number of young raised was compared among study areas and years with a two-way analysis of variance. We chose $P < 0.05$ as the level of significance.

Adults were captured with a variety of traps including bal-chattris, noose poles, and mist nets (Bull 1987). We used 22-gm transmitters (AVM Instrument Co., Ltd., SM1, L Module) attached to the owl's back with a back-pack harness of 6-mm tubular teflon ribbon. Transmitter signals lasted 242-505 days.

Radio transmitters were attached to 10 adult males and 13 adult females and were replaced each year, if possible. All radio-tagged adults nested each year. Observation periods of radio-tagged owls were three years for 3 owls, two years for 7 owls, and one year for 13 owls.

We placed transmitters on 33 fledged juveniles which included all the young raised at Spring, Bowman, and Sheep in 1984 and 1985 and 3 young raised at Thomason in 1985. Observation periods of radio-tagged juveniles ranged from one year (30 individuals) to two years (3 individuals). Juveniles were weighed upon capture.

Radio-tagged owls were located from the ground every two weeks from the time they had a transmitter attached until they died, until the transmitter stopped, until we removed the transmitter, or until August 1986. To locate birds we could not find, we flew every two weeks searching within a 50-km radius of the study areas. Birds located while flying were then located from the ground. Locations of each bird were marked on aerial photographs.

Mortality and survival rates were calculated using Mayfield's (1975) method; confidence limits (95 percent) were calculated using Johnson (1979). One juvenile was not included in these calculations because we found only its transmitter on the ground, and we could not determine if the harness had broken or the bird had been killed and the transmitter torn off. We knew the fate of all other birds.

Results

Reproduction

In all study areas, incubation was initiated between 17 March and 17 April (Figure 1). There

was a significant difference in onset of nesting among study areas ($P < 0.05$); owls in Spring nested earlier than owls in Thomason which again nested earlier than owls in Bowman according to an LSD test ($P < 0.05$, $N = 21$ nests). There was no year by area interaction ($F = 1.59$, $DF = 2$, $P = 0.24$) in nesting dates. In addition, some owls in Spring started incubating within three days of the same date each year in 1983-1986.

Brood size averaged 2.3 ($SD = 0.87$, Table 1). Brood size at 45 nests did not differ among study areas ($F = 0.10$, $DF = 2$, $P = 0.90$) or years ($F = 1.73$, $DF = 4$, $P = 0.17$), and there was no year by area interaction ($F = 1.74$, $DF = 7$, $P = 0.14$). We observed 8 broods with one young, 20 broods with two young, 15 broods with three young, 1 brood with four young, and 1 brood with five young.

All radio-tagged adults nested every year of observation. Of 64 nesting attempts, 77 percent of the pairs successfully fledged young (Table 1). No differences were found in nesting success among study areas ($P = 0.97$). Of the 15 pairs that failed to raise young, 9 failed during incubation, 4 failed with nestlings, and 2 were unknown.

We know of three pairs that renested after their first nesting attempt failed. These females renested 17-20, 28, and 30 days after nest failure, respectively. Of the three renesting attempts, only one was successful. In a fourth case, a female failed during incubation (egg shells on ground) and a new female (with transmitter) laid eggs on the abandoned nest 13-15 days after the first female left it. We did not know if the first female renested or if both females were mated with the same male as only one male was observed.

Young left the nest 52-74 days ($\bar{x} = 62$, $SD = 4.34$, $N = 18$ nests) after females started incubation. Assuming incubation lasted 36 days (Mikkola 1981), the mean number of days in the nest was 26 ($SD = 4.34$, range = 16-38 days, $N = 18$ nests). Even though there was a significant year by area interaction in fledging dates ($F = 3.29$, $DF = 5$, $P = 0.02$), the major difference was among study areas ($F = 6.11$, $DF = 2$, $P = 0.01$) and not among years ($F = 2.22$, $DF = 4$, $P = 0.10$). The significant interaction resulted from 1983 when the fledging dates were approximately the same in all areas. We think owls in Bowman, Sheep, and Thomason nested earlier in 1983, because there was less snow that

STUDY AREA

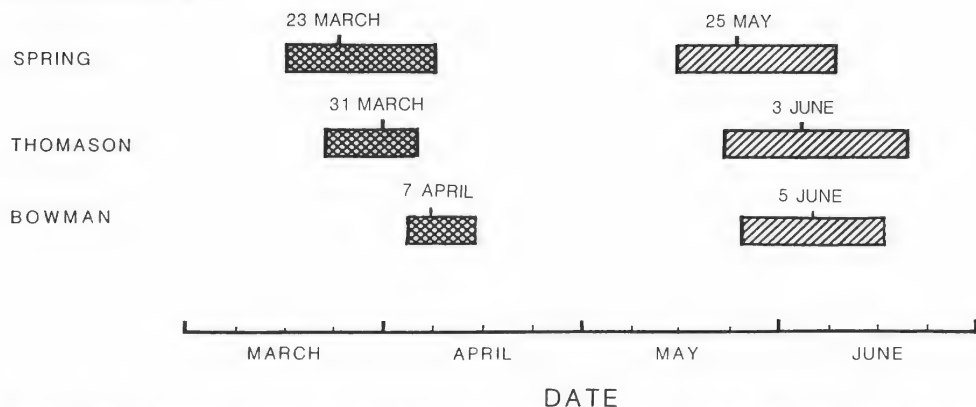


Figure 1. Nesting phenology of great gray owls in three study areas in northeastern Oregon, 1982-1986. Sample sizes were 13 nests in Spring, 5 in Thomason, and 3 in Bowman for the onset of incubation, and were 19, 10, and 6 nests, respectively, for dates young left the nest. Mean dates are identified for incubation and fledging periods.

TABLE 1. Productivity at great gray owl nests by study area in northeastern Oregon, 1982-86.

Study area	Nesting pairs N	Pairs that raised young (%)	Brood size		
			$\bar{x}$	SD	Range
Spring	29	76	2.4	0.94	1-5
Thomason	19	79	2.3	0.91	1-4
Bowman	10	80	2.1	0.64	1-3
Sheep	6	67	2.0	1.00	1-3
Total	64	77	2.3	0.87	1-5

year than in the other years of the study. Owlets in Spring fledged earlier than owlets in Bowman and Thomason which were not different (LSD, $P < 0.05$, $N = 34$ nests).

For first annual nesting attempts, young left the nest between 14 May and 19 June. Young of renesting females left the nest between 22 June and 18 July. Owlets left over a period of several

days, with the largest nestling usually being the first to leave. We never observed all young in a nest leaving on the same day. Five young in one nest left over a period of eight days. The mean weight of young when they left the nest was 609 g ($SD = 75.08$, range = 360-755 g, $N = 81$).

Twice we observed the adult owls favor the weakest of the fledglings. At one site where three young had left their nest, one young was blind in one eye, uncoordinated, and gurgled instead of hissed. The female stayed nearest to the blind owlet and the male fed it more frequently than the others. In another case, one of two fledglings was temporarily injured in handling and the female stayed with that young for several days until it could fly again.

After the young left the nest, the female stayed near their young, and the male continued to feed both the female and young. Usually after several days, the male took prey directly to the young and the female caught her own prey. Some females also caught prey for their young. After 3-6 weeks, 11 of 12 females were more than 1 km

from their young and had apparently left the care of the young to the male. One female remained near the male and young for several months. Males continued to feed the young for more than three months after young left the nest. After three months, the young started to catch prey on their own.

We observed one exception to this pattern. At one nest, a female took over the care of her young when the male stopped delivering food (a few days before the owlets left the nest). Two young were in the nest at the time and left the nest 30 days after hatching. When they left the nest their weights were 360 and 530 g, which were well below the average weight of 609 g (CL = 592-626). The smaller owlet died several days later. The female continued to feed the juvenile for at least two months. During this time the male was alive and within 4 km of the nest, but we did not observe him feed the female or young.

Breeding Age

We followed 19 one-year-old owls and 3 (1 female, 2 males) two-year-old owls with transmitters, and none of them nested. One of the two-year-old males was with a female during the nesting season, but they did not nest. Two owls banded as fledglings were later found nesting as a two-year-old female and a three-year-old male at separate nests. Thus, great gray owls probably rarely breed at one year, sometimes at two years, and more commonly at three years.

Nest Failures

Cause of nest failures was varied. Broken eggs (uneaten) were found on the ground below two nests; they had apparently fallen through the nest. A nestling several days old was found dangling from a lichen below another nest. Single dead nestlings were found on the ground below two nest trees and had apparently fallen out. Two nests contained addled eggs and were abandoned following incubation of 26 and 42-48 days, respectively. Twelve nests were lost to unknown causes; however, we suspect common ravens (*Corvus corax*) destroyed most of them as we found broken egg shells within 100 m of four of them. A feather from a great horned owl (*Bubo virginianus*) was found in a great gray owl nest shortly after the nestlings disappeared, suggesting that the cause of failure was great horned owl predation.

Mortality of Adults and Juveniles

One of 10 adult males and three of 13 adult females died during the observation period. Using Mayfield's method (1975) the annual probabilities of survival for adult nesting males and females were 0.91 (CL = 0.78-1.00) and 0.84 (CL = 0.70-1.00), respectively. Cause of death could not be conclusively determined; however, one bird had been plucked in a tree, indicating avian predation; one bird had the head eaten and the remainder of the body buried; the remains of one bird included a wing, the transmitter, and avian fecal material; and one bird had not been eaten. All the deaths occurred in the fall or winter.

Of 33 juvenile owls with transmitters, 9 died before they became independent of the adults, 5 died in the fall, and 1 died after it was a year old. Using Mayfield's method (1975) the probabilities of a juvenile surviving the first 12, 18, and 24 months were 0.53 (CL = 0.44-0.75), 0.39 (CL = 0.24-0.65), and 0.31 (CL = 0.16-0.57), respectively. We concluded that great horned owls and northern goshawks (*Accipiter gentilis*) killed seven of the dependent juveniles based on plucked feathers and fecal material at the kill site. We also saw a great horned owl fly from a tree containing the carcass of a dead juvenile. Two juveniles apparently starved to death during the period parents were feeding them. Of the five independent juveniles that died, two died of avian predation, and three died of unknown causes.

We saw red-tailed hawks hit juveniles on two occasions. One of the juveniles was carried a short distance before it was dropped unharmed.

Discussion

Timing of incubation appeared to be related to elevation because the owls started incubating earliest at Spring, the lowest site. The study areas at higher elevations usually had more than 0.5 m of snow (reduced prey availability) in March while snow was usually gone by mid March in Spring. Franklin (1987) found that the date the first egg was laid was significantly correlated with snow depth at the onset of the breeding season. Other factors such as prey density or age of breeding owls may have differed among the study areas and affected the nesting dates; however, we have no data on this.

Timing of incubation and egg size in this study did not differ appreciably from results reported in other studies. Female great gray owls have been reported on eggs every month from March until June (Nero 1970, Collins 1980, Pulliainen and Loisa 1977, Winter 1986, Franklin 1987).

Franklin (1987) found that clutch sizes in North America were significantly smaller than those in Scandinavia; he also reported an annual mean brood size of 2.7 and 3.0 in southeastern Idaho and northwestern Wyoming. Mean brood size in this study ($\bar{x} = 2.3$) was lower than Franklin's and lower than the 2.9 (range = 1-7) reported for great gray owls in Finland and Sweden (Mikkola 1981). Productivity at nests did not differ among years or study areas in this study. Franklin (1987) did not observe annual differences in productivity either, unlike the annual variations observed in Scandinavia, which were attributed to fluctuations in vole populations (Mikkola 1981). Nest success in this study was 77 percent; Franklin (1987) reported a nest success of 70.5 percent in Idaho and Wyoming.

Length of time in the nest has been reported elsewhere as 18-25 days (Höglund and Lansgren 1968), 20-29 days (Mikkola 1983), and 3-4 weeks (Nero 1984). Some of the young we observed were in the nest longer than previously reported.

Our observations suggest that adult great gray owls sometimes favor the smaller or weaker of their offspring. Nero (1970) observed similar behavior. These observations are contrary to the theory that the weakest are not attended in many raptors if resources are scarce (Newton 1979). However, if resources were not limiting in this situation, it would seem advantageous to produce the maximum number of offspring possible.

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Our observation of females leaving the young 3-6 weeks after the young have left the nest has not been reported elsewhere. Both Nero (1980) and Mikkola (1983) reported that both parents stayed with the young for up to three months after fledging. We think females left to replenish their fat reserves or restore body condition. None of them renested. The one female we observed stay with the young probably did so because the male had quit feeding the young.

The high juvenile mortality observed in this study appears to be typical of great gray owls (0.53 mortality rate for first 12 months). No other mortality rates are available in the literature, although Mikkola (1981) reported that a large proportion of juveniles perish.

If juveniles survive to breeding age (2-4 years), annual survival rate is high for nesting adults (0.84 and 0.91 for females and males, respectively). Because we observed such low mortality for adults and observed many adults nesting each year of this study (5 nesting seasons), we think great gray owls are long-lived (10 to 20 years).

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RESEARCH NEWS AND COMMENTS

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Yellowstone Fires: A Preliminary Report

The fires of the Greater Yellowstone Area (GYA) were almost daily national news in July, August, and September of 1988. The fires were described in many ways: a national tragedy, a natural wonder, a unique research opportunity, the most significant ecological event in the history of the national parks, a policy disaster, and nature exercising its prehistoric right to make over landscapes.

Now that the fires are out, it appears that they might best be characterized more simply as a big surprise. Managers and their scientific advisors on U.S. Forest Service (USFS) and National Park Service (NPS) wilderness lands in the GYA were surprised by the magnitude of fires that exceeded all imagined scenarios built into their respective natural fire management plans. The nation's foremost professional firefighters were surprised to see fires exhibiting behavior and power that the best fire behavior models failed to predict. Most Americans, including the President of the United States, were surprised to discover that there even was such a thing as a natural fire policy. Certainly the media were caught by surprise; their coverage of the fires proved so uneven and confused that after-the-fact reporting on the fires, now appearing in many magazines, frequently devotes substantial ink to correcting misimpressions developed by daily media reports during the fires.

We seem now, at the end of 1988, to be past the stage of frequent surprises. As an assortment of independent panels, interagency commissions, and other government teams go about the analysis of the fires, fire policy, and fire fighting procedures, bureaucratic routine and process replace nature's whimsy. But lack of surprises should not lessen interest in Yellowstone's extraordinary fire season, especially among mem-

bers of the scientific community. The fires, as several observers have noted, are only the first act of the play, and there promises to be a lot of drama yet to come.

Fire Management History

Since early in this century, plant ecologists have recognized the significant role of naturally caused fire in many forest communities. Prior to the arrival of Europeans, fire (set by lightning or by native Americans) was nearly as important as soils and climate in determining the condition and composition of many plant communities. Fires burned patches, sometimes small, sometimes large, of vegetation in irregular patterns, creating and maintaining habitat diversity for plants and animals. North American landscapes were in fundamental ways the products of fire.

Fire suppression was the order of the day on both public and private lands until relatively recent times, when several federal agencies began to experiment with prescribed (that is, intentionally allowed, whether human or lightning-caused) burns. The USFS began using human-set prescribed burns as a silvicultural tool in a few areas in the Southeast in the 1940s, for the purposes of removing low-value growth or generating new even-age growth. In 1970, the USFS began to permit lightning-caused fires to burn on some wildlands in order to preserve wilderness values, which were closely identified in the public mind with the natural processes of primitive wildlands.

The NPS, with its more wilderness-oriented legislative mandates, was more aggressive in attempting to reestablish the role of natural fire in its wilderness settings. Managers began actively experimenting with human-set prescribed burns in Everglades National Park in 1958 to

protect pine forests from incursions of hardwoods. In 1968, after several years of experimentation with small human-set prescribed burns, Sequoia National Park established a natural fire program, and by 1978, twelve areas in the National Park System had programs to allow at least some naturally caused fires to burn. The goal of these programs differed from that of early USFS programs in that a state of primitive wildness—and resulting species diversity and dynamic processes—was of primary importance rather than the production of lumber.

The GYA includes roughly 12 million acres in northwestern Wyoming, southcentral Montana, and east central Idaho. Yellowstone National Park, a 2.2 million acre reservation at the center of the GYA, initiated its Fire Management Plan in 1972, with 340,000 acres of backcountry designated for natural fire burns. By 1976, about 1.7 million acres within Yellowstone Park was included within natural fire zones. Yellowstone Park's Fire Management Plan required suppression of all fires that showed risk of threatening human life, property, historic and cultural sites, specific natural features, or threatened and endangered species. Human-caused fires were all subject to immediate suppression, and the Fire Management Plan gave park managers the option of starting fires for purposes of research or to speed up the natural process.

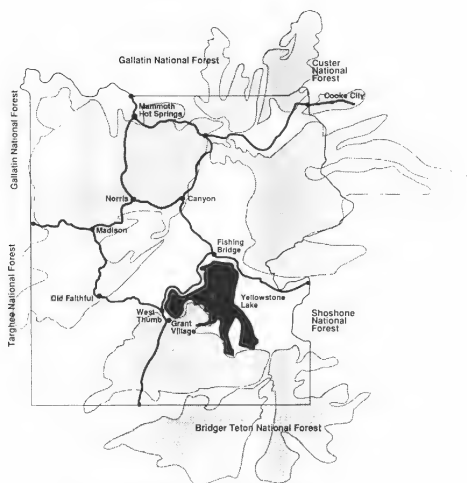
There has been considerable confusion in the media over the extent and effects of fire suppression in Yellowstone. The first known federal involvement in fire fighting occurred in the then fourteen-year-old park in 1886, when the U.S. Cavalry was assigned to its protection. One of their first duties was to fight a fire burning near Mammoth Hot Springs, park headquarters, in the northern part of the park. From that time on until the early 1970s, the goal of management was to suppress any fires, whether they were natural or human-caused. Fire suppression on the park's northern range, a mixed grassland/sageland region making up less than 20 percent of the park, has been largely successful for nearly a century. A fire cycle—that is, the rate at which natural fires recur—of 25 to 100 years has been documented on some portions of the northern range. Consequently, fire suppression there has been underway long enough to have noticeable effects on plant communities.

On the other hand, fire suppression in the rest of the park, which was largely covered by forests, was much more difficult. It was easier to reach and suppress fires on the northern range than in the vast forests that cover most of the park, and so firefighting in the forests was not consistently successful until after World War II, when aerial fire fighting technology became available, thus allowing easier movement of men and equipment to fires in hard-to-reach backcountry areas.

The fire cycle in the forests has been determined through tree-ring studies to be 250 to 400 years. This is of course a much longer fire cycle than that on the northern range, and is also a far shorter period of effective fire suppression. But the differences in fire cycles in different parts of the park have escaped the notice of many media, and the short fire cycle and long history of fire suppression on the northern range have often appeared in the media as applying to the entire park. This has led to unfortunate generalizations about “unnatural buildups” of forest fuels because of fire suppression in the park. In fact, fire suppression in the park forests over the years since World War II may not have made much difference in fuel levels. Older stands of lodgepole pines quite naturally contain substantial levels of dead and down trees, which have been described incorrectly as unnatural or abnormal by both agency personnel and reporters.

Fire Management in the GYA

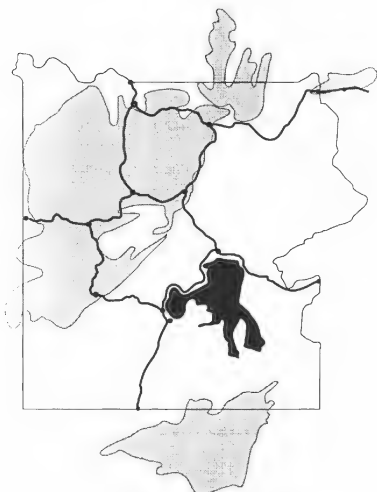
Within the GYA are portions of 6 national forests, 2 national parks, and 2 national wildlife refuges. In the past fifteen years, substantial progress has been made in coordinating ecological management across agency boundaries; part of the progress was development of agreements between the Park Service and some neighboring forests regarding the acceptance of each other's natural fires. In principle, this meant that a natural fire starting on one agency's land could be monitored jointly and could conceivably be welcome to cross the boundary. In fact, there were considerable differences in definitions between the agencies over what was an acceptable size fire and what was acceptable fire behavior. The Park Service's definition of acceptability was aimed at accommodating potentially much larger fires than the Forest Service's. Generally, the



A. Total burned areas.



B. Prescribed burn fires



C. Human caused.



D. Natural fires originating outside Yellowstone Park

Figure 1. Background to fires affecting the Greater Yellowstone Area. A. total burned areas of the Park (shaded). B. extent of natural fires originally managed as prescribed burns under the YNP Fire Management Plan. C. extent of human-caused fires originating outside of YNP, but spreading into the Park. D. extent of naturally caused fires originating outside of Yellowstone National Park, but spreading into the Park.

Forest Service had much tighter restrictions on fire; the Forest Service's system required that fires be suppressed under climate and fuel conditions that the Park Service still found tolerable for allowing fires to burn, and the Forest Service set absolute maximum acreages (1,000 acres in Shoshone National Forest east of YNP, for ex-

ample) on their fires. Any fire that showed a threat of growing beyond that size was suppressed immediately. Both the new strengths and remaining weaknesses of interagency cooperation would be highlighted by the fires.

In the first sixteen years of the Yellowstone plan's existence, 235 fires were permitted to burn

in the park under the terms of the plan (thousands of lightning strikes were observed to go out without burning any measurable acreage). A total of 34,157 acres was burned. The largest single fire burned 7,400 acres. Only 15 burned more than 100 acres, and most burned an acre or less.

The program was viewed as a success in many ways—restoration of fire as an ecological force, education of the public regarding natural systems, increased research opportunities—and the experiment was yielding significant information on fire ecology in Yellowstone vegetation types. In fact, only months before the fires of 1988, a preliminary research report by Dr. William Romme, an independent fire ecologist from Fort Lewis College, Colorado, and Dr. Don Despain, NPS plant ecologist, suggested that the Yellowstone area fire regime involved many small fires interspersed every 200-400 years by massive fires that swept across large portions of the park. Romme and Despain concluded that “Another major burning cycle may begin within the next century, as extensive areas are now developing flammable late successional forests.” The fires of 1988 were not a big surprise to quite everybody.

Climate and Fire Conditions

The Rocky Mountains were in a drought through most of the 1980s. The driest previous year in the history of the Fire Management Plan was 1981, when prescribed fires burned 20,240 acres.

The GYA experienced a peculiar weather pattern during the drought. In the period 1982-1987, annual precipitation was well below average, but the shortfall (so to speak) occurred in winter. Summers during these years were unusually wet. Precipitation in July averaged about 200 percent of normal over 1982-1987. Summers are normally dry in the GYA, so 200 percent of very little is still very little. But it was more than enough to dampen natural fuels. From 1982 to 1987, while much of the West struggled with a famous and economically stressful drought, natural fires in Yellowstone Park only burned about 1,000 acres.

Part of the lesson being learned from the Fire Management Plan was that typically fires will burn a little bit here and there, but that there is an imaginary line or threshold, a combination of conditions produced only in extremely dry

years. Once that threshold is crossed, fires will grow much more dramatically, and burn a lot more landscape. One of the biggest lessons of the 1988 fire season was that that threshold is difficult to identify and the experts disagree on where it is. Disagreements aside, one thing was clear: once the threshold is crossed, the fires will not be stopped by conventional fire fighting, and may burn a whole lot more landscape than managers anticipated or hoped for.

The 1988 Fire Season

Monitoring of fire conditions began in early April, when USFS and NPS fire specialists activated their regular system of fire indices. Well-established conventions in the firefighting community include measurement of a wide variety of conditions, including moisture content of various fuels, man- and lightning-caused fire risks, spread component (a measure of the speed with which a fire would travel if started), energy release component (a measure, in simplistic terms, of how hot a fire burns, which affects what sort of fire fighting equipment must be available), and others. By June 15, eighteen such indices were being computed daily at twelve locations in the park. By July 1, they were being computed at twenty-six locations. An unfortunate and misleading implication of the term, “Let-burn policy,” used both within and without the agency, is that managers put their feet up in their office and do nothing. Quite the contrary; monitoring is a major, daily occupation during any fire season.

The fire season began normally. Long range drought indices suggested that the GYA was in at least a moderate drought by the end of April, but local conditions in the park revealed the complexity of interpreting such information. Rainfall was above average in April (155 percent of normal) and May (181 percent). During late May and June some twenty fires started, and 11 went out on their own. The others behaved more or less as fires had in earlier years. But June rainfall was only twenty percent of normal; sometime in early July, it appears, the theoretical threshold mentioned earlier was crossed.

The critical period of decisionmaking, as identified by post-fire review boards, managers, and other observers, was roughly July 1 until July 21. By July 15, when a total of 8,600 acres had



Figure 2. Satellite view of fires on 7 September 1988. Besides the fires in the Greater Yellowstone Area (upper corner of Wyoming), other fires are visible in Idaho (upper left), Utah (lower center), and smoke from a major Montana fire crosses the top of the image.

been burned in the park, NPS and USFS fire specialists and administrators were aware that weather conditions were extremely dangerous, but it remained unclear to many just what the danger meant. On July 21, NPS managers decided to suppress all existing and new fires as resources would allow. On that day, the total perimeter of all fires enclosed a little less than 17,000 acres.

It is unlikely that the extreme dryness alone would have been enough to create the situation that next developed. In July, August, and September, a series of six dry cold fronts passed through the Yellowstone area, with winds of 40 to 60 miles per hour that fanned the fires and

moved them great distances very quickly. It was during these episodes of high wind that the fires performed most spectacularly, and ate up the most fuel.

Extreme fire behavior became nearly the order of the day, as fires ran as much as 10 miles in a day, sending embers as much as a mile and a half ahead of the main fire to create dozens of "spot fires." The presence of so many spot fires, along with the rapid and wide advance of the main fires, made it impossible to fight the fires head-on without risking many lives. Hundreds of miles of fire lines were constructed, but with the spotting behavior fires routinely jumped usual barriers such as rivers and roads. Standard

hand- or bulldozer-built lines were no barrier at all. Among the examples of black humor (an appropriate term, if ever there was one) with firefighters was, "What's black on both sides and brown in the middle?" The answer: a bulldozer line in Yellowstone.

Fire experts found themselves using terms like "slopover" to describe a huge 15,000-acre burn that appeared on the edge of the North Fork Fire. The scale of the fire events regularly exceeded projections, until to many the entire summer had an unreal quality.

By September 26, the perimeter of burns in the GYA was 1.38 million acres. Fifty fires had been ignited by lightning, of which eight were still considered alive, though after that date they made no more of the dramatic runs that had been seen during the summer, when thousands of acres of forest were eaten up in hours. At the peak of fire fighting efforts, 9,500 firefighters (civilian and military), dozens of helicopters, and more than 100 fire trucks from many states were involved in a massive interagency struggle with the fires. The cost is now estimated at about \$120 million.

Media attention, and to a great extent fire suppression efforts, concentrated on the protection of various developments in the park and communities nearby. The resultant media coverage was perhaps inevitably confused, as so many stories and issues were under attention at once that any brief report was almost certain to muddle them. A brief chronology of the major fires may help set the stage.

Major Fires

The huge North Fork fire, whose perimeter eventually exceeded 500,000 acres, was a human-caused fire started on June 22 in Targhee National Forest just west of Yellowstone National Park (none of the human-caused fires in the GYA in 1988 originated as prescribed management-set fires; they were all accidental fires, fought from the outset). It quickly burned into the park and eventually threatened developments at Old Faithful, Madison Junction, Norris, Canyon Village, Mammoth Hot Springs (NPS headquarters), and Tower-Roosevelt, and the communities of West Yellowstone, and Gardiner, Montana.

The Shoshone Fire, a naturally caused fire, started in southern Yellowstone Park on June 23 where it was managed as a natural fire. It grew to a perimeter of more than 24,000 acres before being administratively redefined as part of the Snake River Complex of fires, whose total perimeter acreage was more than 172,000. By then it had threatened Grant Village, a park development on the shore of Yellowstone Lake.

The Storm Creek Fire, a lightning fire started on July 3 on the Custer National Forest north of Yellowstone Park, was at first managed as a prescribed natural fire under the terms of the national forest's fire management plan, but after two weeks was redefined as a "wildfire," that is a fire no longer within management prescriptions. It was then fought, but grew to a perimeter of 95,000 acres and threatened the communities of Silver Gate and Cooke City, Montana.

The Clover/Mist Fire, started by lightning on July 9 in eastern Yellowstone Park, was originally managed as a prescribed natural fire under the terms of the park's fire management plan, then was fought. It grew to a perimeter of more than 319,000 acres in the park and in Shoshone National Forest east of the park, and showed signs of threatening Silver Gate and Cooke City, then ran east and burned several structures in the Crandall/Squaw Creek area of Wyoming.

The Hellroaring Fire, a human-caused fire started on August 15 on the Gallatin National Forest north of Yellowstone Park, eventually burned a perimeter acreage of 66,000 acres.

The Huck Fire, a human-caused fire originating on August 20 on the John D. Rockefeller Memorial Parkway between Yellowstone and Grand Teton National Parks, eventually grew to a perimeter of more than 106,000 acres before it was administratively redefined as part of the Huck/Mink Complex, whose total acreage was more than 228,000. It required the evacuation of Flagg Ranch, a development just south of Yellowstone Park.

Several smaller fires added to the total acreage. Merely that the Fan Fire, for example, which burned a perimeter of 21,000 acres in Yellowstone Park, can be referred to as a "smaller" fire suggests the tremendous scale of this event.

Even the most casual reading of this summary of the major fires will reveal the extent to which

this was an interagency emergency, as well as the extent to which the fires were managed under a variety of policies. Public perception, created largely by the media, was simpler.

In many media reports, especially on television, all fires were usually referred to as the "Yellowstone fires." Of course they all did occur in the GYA, and thus were more or less Yellowstone fires. But to the public, "Yellowstone" means Yellowstone Park, and the distinction between fires on NPS land and those on USFS land was easily lost. As a result, all the fires, including those caused accidentally by humans and those caused by lightning in national forests near the park (these two categories include five of the seven largest fires in the GYA), were frequently attributed to the NPS Fire Management Plan. There was a common public misconception that all of these fires were, in other words, the result of the park service's policy of letting fires burn.

There was also confusion over the Fire Management Plan. The NPS "let-burn policy" was blamed (in interviews with local citizens, in the statements of politicians, in editorials, and in some hilarious political cartoons) for the continued growth of the fires throughout the summer and fall, with the implication that the NPS continued to allow the fires to burn, though full suppression was the order of the day after July 21. Television coverage of evacuations of developments and nearby communities was regularly linked to discussions of NPS fire policy, when only one park development, Grant Village, was evacuated because of a fire originating as a natural fire under the NPS Fire Management Plan. All other evacuations in or near the park resulted from human-caused fires. Thus it was that NPS fire policies appeared solely responsible for what was reported as a giant management fiasco and ecological tragedy.

One of the many fascinating consequences of the fires does involve media handling of the story. The Yellowstone fires have few equals among natural resource issues for the amount of media attention they generated. Among the investigators studying the enormous amount of material generated in the press and electronic media is Dr. Conrad Smith of the Ohio State School of Journalism, who is conducting quantitative studies of emphasis and accuracy in both agency information handling and media reporting

during the fires. His preliminary work suggests to him a gradual improvement over the course of the summer in the quality and accuracy of reporting; perhaps both agencies and media can benefit from this sort of analysis.

Effects and Aftereffects

Public interest in the GYA, especially in Yellowstone Park, following the fires has amounted to a heartwarming outpouring of sympathy and offers of support. It has been estimated that as many as 30 percent of all Americans visit Yellowstone during their lives, so the park is familiar to many million people. Numerous corporations, institutions, organizations, and individuals have offered help of one kind or another. Much of the help offered is inappropriate, such as pledges of non-native seedlings from other parts of the country, but the agencies involved recognize the most important fact in this public reaction: Yellowstone is a remarkably well known and loved place. NPS and USFS officials have established offices to deal with offers of assistance, and to channel them in meaningful directions.

This array of public interest, some informed and some not, points up the challenges faced by agencies in what is awkwardly called the "recovery" process. For the USFS lands where timber harvests or other commercial uses may prevail, there is indeed something to recover from. Active reseeding and revegetation may be useful in some places. For NPS lands where visitor facilities such as trails, picnic areas, or buildings were damaged, recovery also seems an



Figure 3. In the foreground is a thirteen-year regrowth of lodgepole pine following a 1954 fire in YNP. This picture was taken in 1967. NPS photo by J. R. Douglass.

appropriate word. But for the large areas of wilderness burned by natural fires, recovery is by definition the job of nature. Rhetoricians even argue that it is inappropriate to describe a naturally burned forest as one in need of recovery at all; it is merely a forest in a different stage of its life, a stage through which it passed many times prehistorically, during previous fire cycles.

But the language of recovery is not easily dismissed. Both managers and commercial interests hoping to persuade potential visitors that Yellowstone is still worth seeing are relying heavily on a "rebirth rhetoric," emphasizing the esthetic excitement of seeing the GYA "come back to life," when at least the Yellowstone Park portion of the GYA has just experienced an especially active stage in its primitive life, of which fire was a major element.

Recovery needs, that is actual physical work to be done, are indeed extensive in both Yellowstone Park and in surrounding national forests. In the GYA some 850 miles of hand-dug firelines had to be restored, to avoid erosion and incursions of exotic plants on exposed soils. About 137 miles of bulldozer lines (32 in Yellowstone Park) needed similar treatment. Dozens of "spike camps," helicopter landing sites, and hundreds of smaller disturbances also needed to be repaired. In many instances, the efforts of fighting the fires created more enduring disruptions of settings than did the fires. Much of the work of



Figure 4. Bulldozer damage. It is a common expression among fire ecologists that fire suppression activities can do longer-term damage than the fire itself. In 1943, this bulldozer line was dug near Lewis Lake in southern YNP. Thirty years later, when this photo was taken, native vegetation had made little progress in recolonizing the cut; non-native grasses planted on the cut in 1943 remain the only significant cover. NPS photo by Don Despain.

restoring fire lines and rehabilitating campsites was accomplished before winter snows came.

Structural losses were light, limited to about 55 small buildings, cabins, trailers, and out-buildings. Other losses included some small bridges, 8 miles of main power lines, numerous picnic areas, and related service areas in the park. There is a widespread if informal feeling that the massive firefighting efforts probably did not significantly reduce the acreage burned, but there is also consensus that firefighter's efforts to protect property and human life were remarkably successful. Firefighting activities resulted in many minor injuries to personnel and one fatality was reported: a firefighter was killed by a falling snag in Wyoming.



Figure 5. Bull elk feeding on unburned grasses in burn area, YNP; wildlife frequently fed and bedded down within sight of fire. NPS photo by Jim Peaco.

Wildlife losses were also light: the large herds of grazing animals that are a major attraction of the GYA displayed behavior not at all like that in traditional portrayals of forest fires, such as the movie "Bambi." Animals were only caught by fires when the fires made fast, wide runs. Most of the time, animals more or less stepped aside. Many photographs and films have already been published of bison and elk grazing calmly in a meadow while the forest behind them burns. Surveys of carcasses in Yellowstone Park revealed 257 dead elk (less than 1 percent of the park's summering population of about 32,000), 9 bison (park population—2,700), 2 moose, and 4 mule deer. Most apparently died of smoke inhalation. Similarly light losses, including at least 6 black bears, were reported on surrounding national forests. No threatened or endangered animals have been reported lost.

Of greater concern has been loss of winter range for ungulates. About 11 percent of the winter range (160,000 acres) in the GYA was burned. Of that 11 percent, 8 was canopy or surface burn in forest, and 3 was either meadow or sage/grassland. On some of the smaller ranges, percentage burned is as high as 50 percent.

By early winter of 1988, some public interest emerged in the possibility of supplemental feeding of ungulates, but the USFS, NPS, and the Montana Department of Fish, Wildlife & Parks (MDFWP) all have expressed opposition to feeding for a variety of ecological and scientific reasons. Their position was supported by an independent panel of ecologists assembled in November to assess the GYA ecological situation.

Supplemental feeding of park wildlife is an engaging issue, part of the complex suite of issues surrounding modern parks and their determined tendency toward nonconsumptive uses of park resources. In most wildlife management situations, winter feeding of animals is recognized as a political and sociological issue rather than as an ecological one. That is, feeding can be used to prevent malnutrition mortality or to manipulate animal movements, but the need to do so is based on human needs—humanitarian concerns to prevent death of animals, or sporting needs to maintain high huntable populations—rather than on any intrinsic need of the animal population. Winter mortality is a reality of virtually all northern grazing herds. In YNP, where the goal is to maintain natural processes, feeding would short-circuit the processes of population control and natural selection that occurred in this setting prehistorically, and thus betray the park's greater goal. Herd numbers fluctuate with environmental conditions, which included primitive fire events on the same scale as the fires of 1988. For this principle alone, feeding was deemed inappropriate.

Other supporting reasons included the existence of many research projects involving park animals, projects whose data bases and results would be seriously compromised by such artificial manipulation; the heightened risk of disease transmission among animals at feeding sites; and the high price tag on such a program, conservatively estimated for the largest herd, the northern one, at about two million dollars.

Political and public pressure in favor of feeding still exists as of 1/89, but it is still too early in the winter for much attention to be focussed on the subject. The heaviest mortality among park animals occurs in late winter. The series of mild winters prior to 1988 have allowed park animal populations to grow, so even a normal winter will result in mortality, especially among elk and bison, that may seem alarming to the uniformed (the elk herd routinely experiences 10 percent mortality during winter). Now that the cameras are focussed, so to speak, on Yellowstone, it can be assumed that any mortality will be of greater public interest than in past years. Park service pundits already are speaking gloomily about the possibility of simplistic media reporting on the agency's "Let-die" policy.

Preliminary mapping suggests that a maximum of 15 percent of the whitebark pine in the GYA was burned; whitebark pine nuts are an important food for grizzly bears, and more study is necessary to determine the effects of the loss on the threatened bear.

There has been general agreement among park scientists and advisors that only for purposes of landscaping around developments (such as to screen service facilities from roadways) should any reseedling be undertaken in Yellowstone Park. Extensive soil testing, done as part of the first reconnaissance mapping in September, showed that less than .1 percent of the soils in burned areas received heats extreme enough to kill seeds, roots, rhizomes, and other regenerative plant parts more than an inch under the surface. By late September, newly-cast lodgepole pine seeds in burned forests were covering the forest floor at densities ranging from 50,000 to 1 million seeds per acre. Yellowstone's long history of regrowing its vegetation following fires seemed sufficient proof for most observers that the park's vegetation would regrow at its own pace.

Other short-term ecological concerns include increased erosion or sedimentation in many streams. Levels of erosion and sedimentation will depend upon the rate and amount of spring snowmelt and precipitation, and ecologists generally agree that the long-term benefits of increased nutrients released by the fires will enrich many aquatic systems. Another concern is the risk of non-native vegetation invading burns,

especially in wilderness areas. This is especially a concern in the hundreds of miles of fireline built during the fires, where native vegetation has been removed or destroyed and soil is easily colonized by new vegetation. Sedimentation, erosion, and invasion by non-native plants will, like the other ecological issues discussed earlier, require long-term monitoring.

Social and Political Consequences

Formal review of the fires, of fire fighting logistics and decisionmaking, and of fire policy, will be underway throughout the winter of 1989. There may be Congressional oversight hearings in late winter.

The fires that involved interagency efforts—that includes all of the large ones—have already been subject to technical review by interagency teams. The findings of these teams are difficult to summarize because each fire was so large, with so many decisions and logistical complications, that each team addressed a unique set of issues. For example, the team evaluating the fighting of the Clover-Fire gave the fire fighting agencies high marks for protecting structures, coordinating military participation, training new fire fighters, safety (“1/3 the normal injury rate”), public relations (coordinating fire activities with local communities), and grizzly bear safety (an unaccustomed hazard for most firefighters not used to having to protect their food at night). On the other hand, the team observed that NPS fire management guidelines did not include “circuit breakers” to tell the agency at what set of conditions it was no longer safe to allow fires to burn, that in several ways communications between the NPS and the USFS were inadequate, and that though the personnel on the fires were qualified, there were never enough of them. One interesting sidelight of these fires is that there were so many of them at once that fire fighting resources were often inadequate, or were shifted from one fire to another as priorities changed.

The fundamental necessity for some kind of natural fire policy seems recognized by most participants in the scientific and political debates now underway. The extent to which fires should be allowed to exercise their primitive prerogatives is hotly debated, and though there appears already to be nearly a consensus among participants in the political and scientific dialogues that

some sort of natural fire policy is necessary, there is great difference of opinion over what it should be. The Yellowstone fires of 1988 revealed the extent to which a policy that seems perfectly workable for many years suddenly can become the center of giant controversy. Critics of the NPS policy say it should have been better designed to anticipate the unusual fire conditions of 1988; defenders of the policy say that building fire policy around the extreme conditions of 1988 would be like a farmer managing his best bottom-land in constant anticipation of a 100-year flood.

A common thread in the current dialogues is the fear that while natural fire may be respected in principle, it will be eliminated in fact. It is easy to imagine that the political process may create a policy that in all respects is a model of approval—that expresses all the affirmative sentiments about the importance of allowing fire to play its natural role in the dynamic processes of the national parks—but that is so restrictive in its “circuit breakers” that in fact no fire of any useful size could ever occur. The sorting out of these details and priorities promises to be one of the most interesting processes the conservation movement has witnessed in recent years.

Even the scientific process of analyzing the fires promises to be stirring, newsworthy, and controversial. For example, during the fires, daily reports gave rough estimates of the perimeters of the burns, emphasizing that as much as half of the area within the perimeter was not burned (media reports typically quoted only the larger number). By late September, these rough estimates said that 1.6 million acres had been included within fire perimeters, 1.1 million of which was within the park. First estimates of actual burned acreage within fire perimeters in the park were arrived at by seat-of-the-pants guesstimates by skilled observers in helicopters. The figure they gave was 440,000. Then in late October the first round of infrared aerial reconnaissance mapping was completed, and it estimated a total burned acreage in the GYA of 1.38 million acres, and within the park of 995,000 acres. Then in early December an EROS satellite image analysis of the burns estimated a burn acreage of 706,000 acres in the park. These numbers, all derived by respected means, differ so widely that further confusion is sure to result.

Differences in methods explain much of the discrepancies. For example, the resolution of the



Figure 6. Aerial view of fire patches. "Mosaic" of burns became the object of fascination for fire fighters and visitors alike by the end of the summer, as winds and vegetation dictated the movements of fires leaving mixed patchworks of black and green across Yellowstone. NPS photo by Jim Peaco.

aerial mapping of October is only 200 acre units. Fires frequently burn in a "mosaic" pattern that creates a variety of shapes and sizes of new wildlife and plant habitats, and quite often the "jigsaw puzzle" is composed of very small pieces, each only a few acres in size. The EROS imagery, on the other hand, is measuring units of burnt or non-burnt land as small as 30 meters on a side.

Also, the helicopter guesstimates, flown in smoky conditions, were rough counts only of burnt forests, while the aerial reconnaissance also measured ground fires under green forest canopies; of the 995,000 acres reported by the IR aerial survey, 367,000 was ground fire under forest canopy, and another 55,000 was meadow or sage/grassland. No doubt upcoming surveys will also differ, and no doubt further public confusion will result.

Opportunities

Promoters of travel to the Yellowstone region are emphasizing the singular opportunity the fires present; only once in several generations can visitors view such a huge ecological unit "star-

ting over" this way. Other opportunities are also presented here; scientific research will certainly burgeon. The park currently hosts some 200 government and independent researchers from many disciplines each year. Yellowstone Park Chief of Research John D. Varley estimates that number may increase by 50 percent.

Opportunities for political haymaking and axe-grinding also abound. The fires have already generated a wild assortment of commentary and polemic, as resource-oriented groups and individuals work to affect public opinion and policy. The very volume and diversity of this flow of talk probably is the best tempering influence on it, and the best guarantee that no one viewpoint will dominate.

But for those who enjoy ecological consequences more than political and social ones, the finest opportunity is the resource's. The biotic communities of the GYA have just received a dynamic jolt of prehistoric dimensions, and all the members of those communities will be doing all that evolution will allow to take advantage of the new order. For nature, opportunity rarely has knocked so loudly in Yellowstone.

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NORTHWEST SCIENCE

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Sixty-second Annual Meeting
of the
Northwest Scientific Association
March 22-24, 1989
Tri-Cities University Center
Richland, Washington

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PROGRAM SCHEDULE

Wednesday, 22 March:

6:00-9:00 p.m. Registration, Shilo Inn

Thursday, 23 March:

Morning

8:00 a.m. Registration

8:50-12:30 Symposium: Biological Resources of the Columbia Basin, South Eastern Washington. Tri-Cities University Center.

Afternoon

1:30-5:00 p.m. Contributed Paper Sessions
Wildlife and Forestry (Auditorium)
Botany and Forestry

Evening

5:00-6:00 No-host social hour. Shilo Inn.

6:00 Banquet Dinner. Shilo Inn.

Friday, 24 March:

8:30 a.m.-4:30 p.m. Contributed Paper Sessions
Wildlife and Forestry
Botany and Forestry
Geology, Meteorology, etc.

1:30-5:00 p.m. Tour of Hanford Site

SYMPOSIUM

BIOLOGICAL RESOURCES OF THE COLUMBIA BASIN SOUTHEASTERN WASHINGTON

Tri-Cities University Center Auditorium, Richland, Washington

Thursday, March 23, 1989

- 8:50 - 9:00am WELCOME - Fred Rose, Tri-Cities University Center.
- 9:00 - 9:20am STRUCTURE AND FUNCTION OF COLD DESERT SPRING STREAMS.
C. E. Cushing. Pacific Northwest Laboratory, Richland,
Washington 99352.
- 9:40 - 10:00am FISHERIES RESOURCES OF THE HANFORD REACH, COLUMBIA RIVER.
D. D. Dauble. Pacific Northwest Laboratory, Richland,
Washington 99352.
- 10:00 - 10:20am NESTING POPULATIONS OF CANADA GEESE ON THE HANFORD REACH,
1953 - 1988. L. E. Eberhardt. Pacific Northwest Laboratory,
Richland, Washington 99352.
- 10:20 - 10:40am POPULATION ECOLOGY OF A SHRUB-STEPPE ELK HERD.
S. M. McCorquodale. Yakima Indian Nation, Toppenish,
Washington.
- 10:40 - 11:00am SEASONAL DIVERSITY AND ABUNDANCE OF HAWKS, OWLS, AND EAGLES
IN THE COLUMBIA BASIN, SOUTHEASTERN WASHINGTON. R. E.
Fitzner. Pacific Northwest Laboratory, Richland, Washington
99352.
- 11:00 - 11:10am (BREAK)
- 11:10 - 11:30am PLANT DISTRIBUTION AND ECOLOGICAL PROCESSES. M. A. Simmons,
J. M. Thomas, and C. M. Panwala. Pacific Northwest
Laboratory, Richland, Washington 99352.
- 11:30 - 11:50am SPRING FLORA OF THE SAGEBRUSH STEPPE EMPHASIZING ECOLOGY AND
ADAPTATIONS. R. J. Taylor. Western Washington University,
Bellingham, Washington 98225.
- 11:50 - 12:10pm RESPONSES OF ARTEMISIA TRIDENTATA AND GRAYIA SPINOSA TO
INCREASING SEASONAL DROUGHT. S. O. Link, M. E. Thiede,
R. D. Evans, J. L. Downs, and G. W. Gee. Pacific Northwest
Laboratory, Richland, Washington 99352.
- 12:10 - 12:30pm RESTORING THE WASHINGTON SHRUB-STEPPE: BASALT WASTE
ISOLATION RECLAMATION PROJECT. C. A. Brandt, and W. H.
Rickard. Pacific Northwest Laboratory, Richland, Washington
99352.

LUNCH BREAK

CONTRIBUTED PAPERS

BOTANY AND FORESTRY

Tri-Cities University Center, Room 117, Richland, Washington
Thursday, March 23

Session Leader: Bryan Valett

- 1:30 - 1:50 pm CARBON ALLOCATION TO REPRODUCTION DURING DROUGHT IN ARTEMISIA TRIDENTATA. R. D. Evans, R. Alan Black, and S. O. Link. Washington State University, Pullman, Washington, and Battelle, Pacific Northwest Laboratories, Richland, Washington.
- 1:50 - 2:10 pm GROWTH AND CARBON ALLOCATION OF RED ALDER SEEDLINGS GROWN OVER A DENSITY GRADIENT. P. Giordano, and D. E. Hibbs. Oregon State University, Corvallis, Oregon 97331-5705.
- 2:10 - 2:30 pm ELECTROPHORETIC VARIABILITY IN WASHINGTON AND BRITISH COLUMBIA POPULATIONS OF CHEATGRASS: EVIDENCE FOR MULTIPLE INTRODUCTIONS. S. J. Novak, and R. N. Mack. Washington State University, Pullman, Washington 99164-4220.
- 2:30 - 2:50 pm FORAGE REDUCTION AND SEEDLING EMERGENCE BY WHITETOP (CARDARIA DRABA) IN THE SAGEBRUSH ECOSYSTEM. L. L. Larson, M. L. McInnis, R. F. Miller, and J. A. Tanaka. Oregon State University, Corvallis, Oregon 97331-5705.
- 2:50 - 3:10 pm ADAPTATION OF THE FOREST-BGC MODEL TO WARM DRY CLIMATES: GROWTH OF PINUS HALEPENSIS IN JORDAN. F. E. Larsen, and S. S. Higgins. Washington State University, Pullman, Washington 99164-4220.
- 3:10 - 3:20 pm BREAK
- 3:20 - 3:40 pm COMPARISON OF HIGH AND LOW THINNING OF WESTSIDE DOUGLAS-FIR: FIVE-YEAR GROWTH RESPONSE. W. H. Emmingham, and L. J. Shainsky. Oregon State University, Corvallis, Oregon 97331-5705.
- 3:40 - 4:00 pm SEASONAL AND DIURNAL TRENDS OF LEAF WATER POTENTIAL FOR YOUNG RED ALDER (ALNUS RUBRA) ALONG A DENSITY GRADIENT IN WESTERN OREGON. S. J. Lu, and J. B. Zaerr. Oregon State University, Corvallis, Oregon 97331-5705.
- 4:00 - 4:20 pm FERTILIZATION AND LIMING OF DOUGLAS-FIR AND NOBLE FIR CHRISTMAS TREES. Donald P. Hanley. Washington State University, Pullman, Washington 99164.
- 4:20 - 4:40 pm INFLUENCE OF FOREST FLOOR ON GROWTH OF DOUGLAS-FIR AND WESTERN HEMLOCK SEEDLINGS WITH AND WITHOUT FERTILIZER. M. A. Radwan. USDA Forest Service, Forestry Science Laboratory, Olympia, Washington 98502.

CONTRIBUTED PAPERS

ZOOLOGY AND WILDLIFE

Tri-Cities University Center Auditorium, Richland, Washington
Richland, Washington
Thursday, March 23, 1989

L. E. Rogers, Session Leader

- 1:30 - 1:50pm CANADA GOOSE BROODING HABITATS ON THE COLUMBIA RIVER BETWEEN CROW BUTTE ISLAND AND RICHLAND, WASHINGTON. M. F. Passmore, and C. Bittler. U.S. Army Corps of Engineers, Walla Walla, Washington, and U.S. Fish and Wildlife Service, Portland, Oregon.
- 1:50 - 2:10pm CANADA GOOSE PRODUCTION ON LAKE WALLULA AND THE LOWER SNAKE RIVER, 1974 - 1988. L. Boe, C. J. Christian, and M. F. Passmore.
- 2:10 - 2:30pm HOME RANGE AND HABITAT USE OF FERRUGINOUS HAWKS IN THE SNAKE RIVER BIRDS OF PREY AREA. D. McAnnis, and M. J. Bechard. Department of Biology, Boise State University, Boise, Idaho 83725.
- 2:30 - 2:50pm FACTORS AFFECTING DISTRIBUTION AND FORAGING OF WINTERING BALD EAGLES ON THE BOISE RIVER IN SOUTHWESTERN IDAHO. R. R. Spahr, and M. J. Bechard. Boise State University, Boise, Idaho 83725.
- 2:50 - 3:10pm COMPOSITION DISTRIBUTION AND MOVEMENTS OF BATS IN SOUTHERN IDAHO. M. C. Whackenhut, and B. C. Keller. Idaho State University, Pocatello, Idaho 83209.
- 3:10 - 3:30pm EIGHT YEARS OF DATA ON THE RELATIVE DENSITY AND SPECIES COMPOSITION OF RODENT POPULATIONS AT THE IDAHO NATIONAL ENGINEERING LABORATORY. B. L. Keller. Idaho State University, Pocatello, Idaho 83209.
- 3:30 - 3:50pm SMALL MAMMAL ACTIVITY AND EDGE USE ON THE SUBSURFACE DISPOSAL AREA, IDAHO NATIONAL ENGINEERING LABORATORY. J. D. Boone, and B. L. Keller. Idaho State University, Pocatello, Idaho 83209.
- 3:50 - 4:10pm RANGE AND HABITAT PREFERENCES OF WASHINGTON GROUND SQUIRRELS. B. J. Betts. Eastern Oregon State College, La Grande, Oregon.
- 4:10 - 4:30pm DISTRIBUTION AND MOVEMENTS OF COLUMBIAN GROUND SQUIRRELS (SPERMOPHILUS COLUMBIANUS) IN UNCULTIVATED HABITAT: ARE HABITAT PATCHES LIKE ISLANDS? B. J. Weddell. Washington State University, Pullman, Washington 99164-4220.
- 6:00 - 7:00pm No-host social hour - Shilo Inn
- 7:00 - 8:00pm Banquet Shilo Inn, Guest Speaker: Jim Chatters will review "Environments and People in Prehistory."

CONTRIBUTED PAPERS

BOTANY AND FORESTRY

Tri-Cities University Center, Room 119, Richland, Washington

Friday, March 24, 1989

Session Leader: Steven O. Link

- 8:00 - 8:20am SEED ZONE TEMPERATURE AND MOISTURE CONDITIONS IN A PARTIALLY FROZEN SOIL/CROP RESIDUE SYSTEM. W. R. Bidlake, G. S. Campbell, and R. I. Papendick. USDA-ARS, Washington State University, Pullman, Washington 98162-4220.
- 8:20 - 8:40am TOXICITY TESTING USING MICROBIAL SYSTEMS. R. C. Rychert. Boise State University, Boise, Idaho.
- 8:40 - 9:00am W-WAVES AND BIOLOGICAL CLOCKS. O. E. Wagner. Wagner Research Laboratory, Rogue River, Oregon 97537.
- 9:00 - 9:20am PLANT SPACING AND W-WAVES. O. E. Wagner. Wagner Research Laboratory, Rogue River, Oregon 97537.
- 9:20 - 9:40am PLANT COMMUNICATION AND W-WAVES. O. E. Wagner. Wagner Research Laboratory, Rogue River, Oregon 97537.
- 9:40 - 10:00 am THE FATE OF DINOSEB-(4-6-DINITRO-sec BUTYL PHENOL IN SEVERAL IDAHO SOIL TYPES AND EXPOSURE HISTORY. T. O. Stevens, and R. L. Crawford. Department of Bacteriology, University of Idaho, Moscow, Idaho 83843.

CONTRIBUTED PAPERS

GEOLOGY, METEOROLOGY, CHEMISTRY, AND MATHEMATICS

Tri-Cities University Center, Room 118, Richland, Washington

Friday, March 24, 1989

Session Leader: Paul Eddy

- 8:00 - 8:20 am METEOROLOGICAL AND HYDROLOGICAL DROUGHT IN WASHINGTON STATE, 1986-88. A. Quinn. Eastern Washington University, Cheney, Washington.
- 8:20 - 8:40 am DEVIL'S KITCHEN AREA AT MOUNT HOOD, OREGON, REVISITED. K. A. Cameron. U.S. Geological Survey, Cascades Volcano Observatory, Vancouver, Washington.
- 8:40 - 9:00 am VIVIANITE FROM KALALOECH, OLYMPIC PENINSULA, WASHINGTON. S. R. Benham, F. C. Tobiason, and M. J. Thielman. Pacific Lutheran University, Tacoma, Washington 98447.
- 9:00 - 9:20 am REINTERPRETATION OF THE ALPINE GLACIAL SEQUENCE IN THE LEAVENWORTH AREAS, WASHINGTON. W. A. Long. 123 River Front Drive, Cashmere, Washington 98815.
- 9:20 - 9:40 am ELECTRON TRANSFER AND RADICAL CATION REACTION RATES OF METHOXLATED BIBENZYLs. G. E. Fryzell, M. Chow, W. A. Rodin, and D. M. Camiaoni. Pacific Northwest Laboratory, Richland, Washington 99352.
- 9:40 - 10:00 am A MATHEMATICAL MODEL FOR THE SPREAD AND CONTROL OF THE AIDS EPIDEMIC. J. S. Palmer, and M. E. Moody. Washington State University, Pullman, Washington.

WILDLIFE AND FORESTRY

Tri-Cities University Center, Room 117, Richland, Washington
Friday, March 24, 1989

Session Leader: Larry Cadwell

- 8:00 - 8:20am ADVERSE CONDITIONING WITH THIRAM TO REDUCE MOUNTAIN BEAVER DAMAGE TO DOUGLAS-FIR SEEDLINGS. D. L. Campbell, and J. Evans. USDA. Animal and Plant Health Inspection Services Science and Technology, Olympia, Washington 98502.
- 8:20 - 8:40am PHYSICAL STRUCTURE, FLORA, AND FAUNA OF MOUNTAIN BEAVER NESTS. M. G. Carey, D. L. Campbell, and C. L. Campbell. USDA Animal and Plant Health Inspection Service, Olympia, Washington 98502.
- 8:40 - 9:00am THE EFFECT OF BEAVER ON STREAM AND STREAMSIDE CHARACTERISTICS AND COHO POPULATIONS IN WESTERN OREGON. K. C. Leidholt, W. McComb, and D. E. Hibbs. Oregon State University, Corvallis, Oregon 97331-5705.
- 9:00 - 9:20am MICROHABITAT SELECTION OF MICROTUS MONTANUS: FEMALE CHOICE. M. A. O'Connell, and J. G. Hallet. Washington State University, Pullman, Washington 99164-4220.
- 9:20 - 9:40am HIERARCHIAL CLUSTER ANALYSIS AS AN AID FOR INTERPRETING HERBIVORE DIETS. M. L. McInnis, L. L. Larson, and M. Vavra. Oregon State University, Corvallis, Oregon 97331-5705.
- 9:40 - 10:00am TIMING AND LOCATION OF ALGAL HOST USE BY AN OLIGOPHAGOUS MARINE HERBIVORE. C. D. Trowbridge. Oregon State University, Corvallis, Oregon 97331-5705.
- 10:00 - 10:10am BREAK
- 10:10 - 10:30am METHODS FOR RELOCATION OF PREY FOR NORTHWEST RATTLESNAKES, CROTALUS VIRIDIS. B. Robinson, and K. V. Kardong. Washington State University, Pullman, Washington 99164-4220.
- 10:30 - 10:50am THYROXINE INDUCED METAMORPHOSIS IN OVERWINTERING TAD POLES OF THE TAILED FROG, ASCAPHUS TRUEI. H. Brown. Western Washington University, Bellingham, Washington 98225.
- 10:50 - 11:10am PLATYRRINE SPECIES DISTRIBUTION AND THEORY OF CORROBORATING EVIDENCE. L. E. Mackelborg, and R. W. Thorington Jr. Washington State University, Pullman, Washington, and Smithsonian Institution. Washington, D.C.

STRUCTURE AND FUNCTION OF COLD DESERT SPRING-STREAMS. C.E. Cushing, Pacific Northwest Laboratory, Richland.

Several ecological studies have been undertaken to learn how cold desert spring-streams function. Studies of primary productivity show that these streams are autotrophic in terms of photosynthesis/respiration (P/R) ratios, but analysis of organic budgets reveals that they have characteristics of heterotrophic streams. The key to this anomaly apparently lies in the severe flash-floods which periodically scour the stream beds, thus acting as "reset" mechanisms. This indicates that the streams should be studied on a flood-to-flood basis, rather than an annual basis. Studies of secondary production reveal that cold desert streams are dominated by collecting detritivores, and that fine particulate organic matter (FPOM) is the dominant food resource. Production in these streams is intermediate between that of hot Sonoran desert streams and streams in warm/mesic temperate regions. Aspects of recolonization, recovery, and succession in these endorheic streams following floods suggests that these processes are mainly governed by stochastic factors, but influenced by deterministic factors.

NESTING POPULATIONS OF CANADA GEESE ON THE HANFORD REACH, 1953-1988. L.E. Eberhardt, Pacific Northwest Laboratory, Richland.

The nesting population of Great Basin Canada geese (*Branta canadensis mollitti*) on Hanford Reach of the Columbia River has been monitored since 1953. The number of nests found was highest during the late 1950's and lowest during the mid 1970's. Population levels have gradually increased over the last decade to a present level of approximately 200 nesting pairs. Geese nest almost exclusively on the 21 islands contained in the Hanford Reach. Dramatic changes have occurred in the usage patterns of the islands by nesting geese over the last 36 years. Prior to 1970, more than half of the nests were located on islands in the upper half of the Hanford Reach. Now, less than 25% of the nesting occurs in the upper stretch of river. Predation by coyotes (*Canis latrans*) is thought to be the major cause of this shift in nesting locations.

FISHERY RESOURCES OF THE HANFORD REACH, COLUMBIA RIVER. D.D. Dauble, Pacific Northwest Laboratory, Richland, WA

The Hanford Reach remains an unimpounded, yet regulated, section of the Columbia River, and thus provides remnant habitat indicative of historic conditions. The fish community is represented by 44 species and 13 families. Within the main channel, cobble substrate and swift currents provide critical habitat for populations of anadromous salmon and resident minnows and suckers. Sloughs and backwater areas are important spawning areas for smallmouth bass and also provide rearing habitat for juvenile fish of all species. The Hanford Reach may contain the only self-sustaining population of white sturgeon in the Columbia River system above Bonneville Dam. Lesser-known fish species of regulatory concern, include the sandroller, two sculpins, and the mountain sucker. Fall chinook salmon are the most important sport and commercial fish species in the Hanford Reach. Numbers of spawning salmon have increased dramatically in the last 20 years, coincident with construction of dams in other portions of the Columbia River and with increased hatchery production and release of juveniles.

POPULATION ECOLOGY OF A SHRUB-STEPPE ELK HERD. S.M. McCorquodale, Yakima Indian Nation, Toppenish.

Reproduction, survival and rate of increase of elk (*Cervus elaphus*) occupying the Hanford Site were studied between 1975 and 1988. During 1975-86, the rate of increase (r) was 0.20; the rate during 1982-86 was 0.30. During 1982-1988, $r = 0.21$ (0.25 if corrected for hunting mortality). During 1983 - 88, 0.77 calves were weaned per adult female in the population. First-year survival was in excess of 0.90 during 1982-88. Population parameters and individual body and antler growth patterns indicated these elk were among North America's most productive and healthy herds during 1975-88.

SEASONAL DIVERSITY AND ABUNDANCE OF HAWKS, OWLS, AND EAGLES IN THE COLUMBIA BASIN OF SOUTHCENTRAL WASHINGTON. R.E. Fitzner, Battelle, Pacific Northwest Laboratory, Richland, WA.

Twentyfive species of birds of prey occur in the Columbia Basin of southcentral Washington. Several species migrate through the area, some overwinter and others utilize the region for nesting. The abundance and distribution of each species is affected by a variety of factors including habitat structure, prey species abundance, mans activities, and the innate behavior of a given species. Several uncommon species are of particular interest due to their state or federal status (ie., endangered or threatened) or the recent expansion of their range. The Barred Owl (*Strix varia*) and Broad-winged hawk (*Buteo platypterus*) are two species that had not been previously recorded in the region. The observational data on Peregrine falcons (*Falco peregrinus*) is also of significance due to the species federal listing of "endangered" in the state of Washington.

RESPONSES OF ARTEMISIA TRIDENTATA AND GRAYIA SPINOSA TO INCREASING SEASONAL DROUGHT. S.O. Link¹, M.E. Thiede¹, B.D. Evans², J.L. Downs¹, and G.W. Gag¹, ¹Pacific Northwest Laboratory, Richland, Washington, and ²Washington State University, Pullman, Washington.

Artemisia tridentata responds to increasing seasonal drought by dropping some leaves and retaining others that are at low activity levels. *Grayia spinosa* is completely drought deciduous. The physiological responses of both species were compared to further elucidate how they respond to increasing seasonal drought. Growth, measured by stem diameter and canopy leaf area changes, was greater for *A. tridentata* than *G. spinosa*. Osmotic potential was lower for *G. spinosa* than *A. tridentata*. *A. tridentata* had lower net photosynthetic rates. *G. spinosa* had lower stomatal conductance. Work was supported by the U.S. Department of Energy under Contract DE-AC06-76RLO 1830.

A METHOD FOR STUDYING THE RELATIONSHIP BETWEEN PLANT DISTRIBUTION AND ECOLOGICAL PROCESSES.

M.A. Simmons, J.M. Thomas, and C.M. Panwala. Pacific Northwest Laboratory, Richland, WA.

The scale at which ecological processes, such as soil moisture, affect plant distribution and growth, have been difficult to measure at the landscape level. Cover estimates for 2 perennial grasses at shrub-steppe grassland sites in Washington and Idaho were analyzed to determine these large-scale relationships. Percentage cover for *Agropyron spicatum* and *Eurotia lanata* were obtained from continuous line-intercept transects of 1000 or 2050 m. Spatial variance and correlation of cover estimates were used to estimate ecological scale, which is defined as the level of resolution providing the most information at the greatest efficiency for a particular phenomena. Functions of sample variance with increasing segment length determine the optimal sampling unit size for percentage plant cover. The distance at which interclass correlation is zero estimates scale, i.e., the physical area in which some ecological process has a statistically meaningful influence. Analysis of spatial variance suggested that transects of 65 to 75 m are appropriate sample sizes for the plants and locations studied. Analysis of spatial correlation showed that transect segments should be dispersed more than 200 m apart to be independent. This analysis was extended to Landsat-5 Thematic Mapper data for one of the sites. Analysis of data from band 4 (0.76-0.90 μ m), with a resolution of approximately 30 m, yielded results similar to cover data.

SPRING FLORA OF THE SAGEBRUSH STEPPE EMPHASIZING ECOLOGY AND ADAPTATIONS. Ronald J. Taylor. Western Washington University, Bellingham, WA.

This will be a pictorial presentation of representative plants and plant communities of the sagebrush steppe, following classifications of Daubenmire. Autecological adaptations of some of the major species will be discussed and threats to native community structure by invasive weeds will be noted.

RESTORING THE WASHINGTON SHRUB-STEPPE:
THE BASALT WASTE ISOLATION RECLAMATION
PROJECT

Charles A. Brandt & William H. Rickard, Jr.
Pacific Northwest Laboratory
P. O. Box 999
Richland, WA 99352

The Hanford Site covers some 145,000 ha of relatively undisturbed shrub-steppe habitat northwest of Richland, Washington. Non-riverine communities are comprised mainly of *Purshia tridentata*/*Poa sandbergii*, *Artemisia tridentata*/*P. sandbergii*, *A. tridentata*/*Agropyron spicatum*, and *Grayia spinosa*/*P. sandbergii*. Since 1976, the U. S. Department of Energy has been conducting extensive studies at Hanford for siting a potential nuclear waste repository. Late in 1987, all repository activities except reclamation were terminated at Hanford. The DOE has committed to restore areas as nearly as practicable to original conditions using native species. Seventy two areas are to be restored to original conditions, including a 23-ha test facility comprising three shafts mined into the north slope of Gable Mountain. Sites were visited to determine whether the existing soil/gravel or vegetative cover would support native species. Sites identified for further work were relieved of gravel or rock overburdens, recontoured to match surrounding topography, and a seedbed was prepared. Native grasses appropriate to each site were planted during October using a furrowing drill. Sites near sources of water will receive supplemental irrigation. Shrubs grown from seed collected on the Hanford Site are to be planted in clumps in March. Sites infested with cheatgrass (*Bromus tectorum*) will be followed for one year prior to seeding.

This work was sponsored by the U. S. Department of Energy under contract DE-AC06-76RLO 1830.

CANADA GOOSE PRODUCTION ON LAKE WALLULA AND THE LOWER SNAKE RIVER, 1974-1988. L. Boe, C.J. Christianson, and M.F. Passmore. U.S. Army Corps of Engineers, Walla Walla, Washington 99362-9265

Western Canada goose (*Branta canadensis moffitti*) production was monitored following completion of 5 dams along the mid-Columbia and lower Snake Rivers. Resultant natural and man-made islands as well as nesting tubs placed along the Snake River were searched twice annually, pre- and post-hatch. These newly created islands offered different nesting habitats compared to pre-impoundment islands. Three islands have supported over 80% of island nesting with gosling production nearly equal to pre-impoundment levels (1,477 hatched in 1988). These as well as properly contoured dredged-material islands supported over 2 nests per acre. Goose tubs maintained throughout the period received little use prior to 1986, but is slowly increasing. Snake River cliffs were searched by helicopter in 1979, 80, and 88 and support up to 1/3 of that area's nesting. Availability of brooding pasture is believed to be sufficient along the Snake River. Decline in brooding habitat quality of a key pasture on Lake Wallula may be a contributing detrimental impact to that local population.

CANADA GOOSE BROODING HABITATS ON THE COLUMBIA RIVER BETWEEN CROW BUTTE ISLAND AND RICHLAND, WASHINGTON. M.F. Passmore and C. Bittler. U.S. Army Corps of Engineers, Walla Walla, Washington and U.S. Fish and Wildlife Service, Portland Oregon.

Movements to and use of brood habitats by goslings were studied during March through May 1983 on Lake Umatilla and Lake Wallula on the Columbia river. One hundred twenty goslings were color dyed in the egg for subsequent observation along the river. Seven aerial flights produced 500 observations of broods, of which 33 contained marked goslings. Most goslings moved downstream from their nest site; maximum movement was 15.3 km. The most heavily used shoreline habitat for brooding was low grass on Lake Umatilla. Lake Wallula geese most frequently used for habitat types (lawn, dense grass, marsh vegetation, and willow/Russian olive). Brood pasture developments are recommended for several areas.

HOME RANGE AND HABITAT USE OF FERRUGINOUS HAWKS IN THE SNAKE RIVER BIRDS OF PREY AREA. D. McAnnis and M. J. Bechard. Dept. of Biology, Boise State Univ., Boise, Id.

Three adult male ferruginous hawks were radio-tracked and visually observed from late May through mid-July 1988 to determine the effects of range fires on home range size and habitat use. The average pre-fledging home range was 7.26 km² (range 4.39-11.99 km²) but increased to 13.13 km² (range 5.71-25.54 km²) during the post-fledging period.

Home ranges consisted of varying amounts of burned habitat. Initial analysis indicates the larger the proportion of burned habitat within the range, the smaller the home range. None of the three males were observed to use habitat types in proportion to their availability.

primary keyword: ferruginous hawk
secondary keyword: home range

FACTORS AFFECTING DISTRIBUTION AND FORAGING OF WINTERING BALD EAGLES ON THE BOISE RIVER IN SOUTHWESTERN IDAHO. R. R. Spahr and M. J. Bechard. Dept. of Biology, Boise State Univ., Boise, Id.

Bald eagles wintering on the Boise River were studied for 2 seasons from 1987-1989. Perch sites and prey capture sites were compared to random sites, and flushing distances to 6 types of human activity were recorded to develop a flushing distance curve. Turbidity and velocity in pools were lower at perch sites than random sites, and the number of perch trees at a perch site was greater than in random areas. Fishermen caused the highest proportion of eagles to flush, followed by walkers, and then vehicles. The 1989 field season is in progress and these data will be analyzed to further describe perch sites and effects of human disturbance on wintering bald eagles. We would like to thank River Run Development company and Boise State University for funding this study.

primary keyword: bald eagle
secondary keyword: habitat

EIGHT YEARS OF DATA ON THE RELATIVE DENSITY AND SPECIES COMPOSITION OF RODENT POPULATIONS AT THE IDAHO NATIONAL ENGINEERING LABORATORY SITE. B.L. Keller. Idaho State Univ., Pocatello.

In 1980, a two-season study of changes in relative density of rodent populations was initiated by snap trapping permanent stations located on widely-separated sites. During 17 sampling seasons, 8,779 specimens of 11 species have been collected in 66,963 snap-trap nights. Mean number of rodents at four similar sites achieved a high of 222.2 ± 51.1 (S.E.) per 1000 trap nights and a low of 63.4 ± 9.0 . Considerable variation was documented in the number of individuals collected among areas both seasonally and among years. The highest single estimate, 347.6 individuals per 1000 trap nights occurred on an area receiving a partial prescribed burn. This area also had the highest fall densities (191.0 ± 34.6 , $n=9$). Density and species composition have declined during dry years. The general pattern of change in rodent composition was largely consistent temporally and among areas but the amplitude of the density achieved in all areas has differed.

COMPOSITION, DISTRIBUTION, AND MOVEMENTS OF BATS IN SOUTHERN IDAHO. M.C. Wackenhut and B.L. Keller. Idaho State Univ., Pocatello.

Eight caves in Lincoln and Gooding Counties were identified as bat hibernacula for Myotis leibii, Plecotus townsendii, and M. yumanensis during winter 1987-88. Summer residents of this area included, Pipistrellus hesperus, Antrozous pallidus, M. lucifugus, Lasionycteris noctavagans, M. evotis and P. townsendii. Five caves on the Idaho National Engineering Laboratory contained hibernating M. leibii and P. townsendii during winter 1987-88. One-hundred and twenty bats were banded at three INEL caves and 417 at caves in Lincoln and Gooding Counties. Limited exchange of bats to adjacent caves occurred at both areas, but no exchange was documented between the two study sites. A fall 1988 survey of five caves showed, 19% of the P. townsendii present were banded, and 95% of the banded bats were using the same cave as the previous winter.

SMALL MAMMAL ACTIVITY AND EDGE USE ON THE SUBSURFACE DISPOSAL AREA, IDAHO NATIONAL ENGINEERING LABORATORY SITE. J.D. Boone and B.L. Keller. Idaho State Univ., Pocatello.

Small mammals were live trapped on a 36 ha site used for shallow land burial of transuranic, activation, and fission products. Information on the effect of additional soil cover, modifications of the perimeter water-diversion dike, and edge use by small mammals was collected for contrast against data published earlier. The minimum number of Peromyscus maniculatus, Microtus montanus, and Dipodomys ordii on grids and trapping lines was significantly lower than found previously. The dike, enlarged and reinforced with large chunks of lava rock, supported a higher density of small mammals than the interior surface. Small mammals preferentially used the edge of the disposal area, a condition that may enhance colonization of disturbed portions of the waste site.

RANGE AND HABITAT PREFERENCES OF
WASHINGTON GROUND SQUIRRELS. B. J. Betts.
Eastern Oregon State College, LaGrande.

Possible locations of Washington ground squirrel colonies in Washington and Oregon were identified from the literature, state data bases, and conversations with local researchers and residents. Squirrels were found at 84 of 167 sites. Most colonies were small; the largest were on protected public lands. Geographic distribution was reduced to about 35% of the historic range. Cultivation seems responsible for range reduction. At 13 locations, 23 habitat variables were measured at 2 randomly chosen sites within a colony and also in a paired non-colony area. Although absolute values for some variables varied greatly between the 13 paired locations, t-tests on the differences in the variables at each area showed that squirrels inhabited sites that had significantly greater percent grass cover, deeper soil, weaker soil, soil with less clay, and less percent litter and cryptogam cover. The latter two differences are thought to be a result instead of a cause of squirrel presence. These results suggest that food availability and soil characteristics are most important in determining where squirrels locate colonies.

CARBON ALLOCATION TO REPRODUCTION
DURING DROUGHT IN ARTEMISIA TRIDENTATA
R.D. Evans, R. Alan Black, and Steven
O. Link. Washington State University,
Pullman and Battelle, Richland.

Artemisia tridentata is unique among desert shrubs because flowering occurs during late summer drought. Inflorescences have higher stomatal conductance than leaves and are capable of positive net photosynthesis during drought. Removing leaves from branches supporting an inflorescence does not alter final inflorescence weight, suggesting photosynthates needed for flowering are produced within the inflorescence. Neighboring leaves are apparently less active photosynthetically than inflorescences as a water conserving mechanism.

DISTRIBUTION AND MOVEMENTS OF
COLUMBIAN GROUND SQUIRRELS
(*SPERMOPHILUS COLUMBIANUS*) IN
UNCULTIVATED HABITAT: ARE HABITAT
PATCHES LIKE ISLANDS? B.J. Weddell.
Washington State Univ., Pullman.

The analogy between habitat patches and islands is examined using data on 1) patterns of patch occupancy and 2) distribution and movements of ground squirrels within and between patches of uncultivated habitat in eastern Washington. Although squirrels moved between habitat patches, colonization of new habitats did not occur, because emigrants settled near other squirrels rather than in vacant patches of habitat. Occupancy was related to distance from a source of squirrels but not to patch area. Because of low colonization rates, ground squirrels may decline dramatically in agricultural regions where they are confined to patchy habitats if patches lose populations through extinction.

GROWTH AND CARBON ALLOCATION OF RED ALDER
SEEDLINGS GROWN OVER A DENSITY GRADIENT.
P. GIORDANO and D.E. HIBBS. Oregon State
Univ., Corvallis.

The structure and composition of developing plant communities is dependent on both the amount and quality of competition between individuals in the communities. In perennial plant communities, this competition is reflected by shifts in carbon allocation among plant parts and can result in long term structural differences between neighboring individuals. Nelder la type density plots of red alder seedlings were planted 4 years ago in the Cascade Head Experimental Forest on the central Oregon coast range of mountains. Throughout the growing season, biweekly growth measurements of stem and branch components were made. Branch samples taken from the plot were destructively analyzed to determine biomass and leaf area. Combining these measurements with regression equations previously developed from the site, parameter values from regression models are used to compare differences in growth and carbon allocation among trees grown at different levels of intraspecific competition.

ELECTROPHORETIC VARIABILITY IN WASHINGTON AND BRITISH COLUMBIA POPULATIONS OF CHEATGRASS: EVIDENCE FOR MULTIPLE INTRODUCTIONS. S.J. Novak and R.N. Mack. Washington State University, Pullman.

Cheatgrass is a cleistogamous winter annual that was introduced almost simultaneously into many locations in the intermountain west during the late 1800's. This weed is now a prominent plant species in numerous habitats throughout this region. The history of introduction, in conjunction with mating system, can influence the genetic variation of an alien in its new range. Our objective was to determine how multiple introductions have influenced the genetic variation of local cheatgrass populations. Seeds from 20 populations were collected from Washington and British Columbia and their genetic variability was analyzed using starch gel electrophoresis. The level of genetic variation in these populations was low, resulting from a selfing mating system. The percent polymorphic loci per population was similar, although distinct multilocus genotypes were observed. These results indicate that different genotypes were introduced into these regions. Some of the patterns of allele frequency variation observed are believed to be due to gene flow subsequent to the initial introductions.

ADAPTATION OF THE FOREST-BGC MODEL TO WARM, DRY CLIMATES: GROWTH OF *PINUS HALEPENSIS* IN JORDAN. F.E. Larsen and S.S. Higgins. Washington State Univ., Pullman.

An attempt was made to assess climatic influences on potential production at several sites in Jordan. Running's FOREST-BGC model was selected as an appropriate tool because of its daily resolution and its apparent general applicability. Four years' weather data, collected at 3 sites, were used to drive the model. The model, with minor adjustments, predicted that insufficient rainfall was available at all sites to support hypothetical stands of *Pinus halepensis* with LAI = 1.5. When water was applied daily, equivalent in quantity to Class A pan evaporation, the model predicted a positive carbon balance for the cooler, high-elevation sites, Amman and Irbid. The low-elevation site, Deir Alla, was too hot to allow positive net photosynthesis after June, even though irrigation maintained soil moisture sufficiently high that base xylem pressure potential after June was at a maximum. These model predictions imply that plant adaptation to high temperature may be as critical as adaptation to drought for those concerned with vegetation management in Jordan.

FORAGE REDUCTION AND SEEDLING EMERGENCE BY WHITETOP (*Cardaria draba* (L.) IN THE SAGEBRUSH ECOSYSTEM. L.L. Larson, M.L. McInnis, R.F. Miller, and J.A. Tanaka. Oregon State University, Corvallis.

Plant biomass and density were measured along 10 permanent and 20 temporary transects to evaluate composition changes associated with whitetop infestation. Regressions were developed relating forage reduction on seeded sagebrush rangeland to increased whitetop infestation. Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) biomass was reduced at a rate of 5.0% for every 100 kg/ha of whitetop biomass ($r^2=0.78$). Whitetop plantings were established in 1986 and 1987 in 3 plant communities with 3 levels of disturbance. Seedling emergence was most likely on tilled soil within annual grass communities.

COMPARISON OF HIGH AND LOW THINNING OF WESTSIDE DOUGLAS-FIR: FIVE YEAR GROWTH RESPONSE. W. H. Emmingham & L. J. Shainsky. Oregon State University, Corvallis.

In young stands of Douglas-fir, small log sizes make it difficult to carry out profitable commercial thinning. Logging costs in a low thinning were over \$100 per thousand board feet more than in a high thinning. Five years later, the low thinning plots showed significantly more basal area and board foot volume growth on a per tree and per acre basis than the high thinning or unthinned plots. Nitrogen fertilization did not increase per acre or per tree growth significantly in either the high or low thinned area.

SEASONAL AND DIURNAL TRENDS OF LEAF WATER POTENTIAL OF YOUNG RED ALDER (*Alnus rubra*) ALONG A DENSITY GRADIENT IN WESTERN OREGON. S.J. Lu and J. B. Zaerr. Oregon State Univ., Corvallis.

Three Nelder plots were established to create a range of densities from 350 to 100,000 trees per hectare. Predawn Leaf Water Potential (LWP) was measured by pressure bomb for seasonal trends and LWP at 2-hour intervals for diurnal trends. Predawn measurements reveal that trees growing at higher densities have significantly lower LWP than those growing at lower densities. The largest differences of LWP between higher and lower densities were found in the latter part of the growing season. Early in the season trees growing at higher densities have lower LWP at night and higher LWP in day time, but later in the season they have high LWP both at night and in the day compared with those growing at lower densities. We conclude that trees growing at higher densities are under greater water stress than those growing at lower densities, especially during the dry season.

FERTILIZATION AND LIMING OF DOUGLAS-FIR AND NOBLE FIR CHRISTMAS TREES. Donald P. Hanley, Washington State University, Pullman, WA.

Douglas-fir and noble fir Christmas trees in Western Washington were treated with fertilizer and lime in order to study the impacts of the treatments and their interactions on tree vigor and current season needle mass. A randomized complete block design was used with 4 locations, 6 fertilizer/lime treatments, and 3 replications at each location for both Douglas-fir and Noble fir. Treatments included lime, 21-0-0, and 10-20-20, each at two application rates. Study statistics that could be observed by growers were selected and included tree height increment, as an indicator of tree vigor, and current season needle weight, as an indicator of tree fullness. Third year results indicated an overall weak statistical significance to the fertilizer/lime treatments for Douglas-fir; a strong influence as to field locations; and a significant association between lime and needle weight for Noble fir.

A MATHEMATICAL MODEL FOR THE SPREAD AND CONTROL OF THE AIDS EPIDEMIC. J.S. Palmer and M.E. Moody. Washington State University, Pullman.

Analysis of the qualitative behavior of our model is in broad agreement with observed trends. The effect of altering the various biological and social parameters incorporated in the model is examined and viral transmissivity, a parameter difficult to ascertain by conventional epidemiological study, is estimated. Using this information the potential for serious spread of AIDS in "low-risk" populations is considered. The possible control of the epidemic by the systematic modification of sexual activity and behavior has been examined. Both time dependent and feedback effects on the behavioral parameters are considered. We investigate three factors which strongly influence the efficacy of behavioral changes to decrease the intensity and overall extent of the epidemic. These are: how soon in the course of the epidemic sexual activity begins to decline, how rapidly the decrease occurs, and to what level does activity finally decline. These results have clear implications for the public health issues raised by the AIDS epidemic. In particular, the model illustrates the dramatic disparity between the number of AIDS cases and the far greater number of infected individuals. As such, behavioral parameters must decrease sharply and immediately if this is to be an effective means of establishing control of the epidemic. Also, a decrease of behavioral parameters in response to the number of infected individuals in the population is more efficient in controlling the epidemic than a decrease in response to the number of reported AIDS cases.

INFLUENCE OF FOREST FLOOR ON GROWTH OF DOUGLAS-FIR AND WESTERN HEMLOCK SEEDLINGS WITH AND WITHOUT FERTILIZER. M. A. Radwan. USDA, For. Serv., Forestry Sciences Laboratory, Olympia, Washington.

A 2-year lathhouse test was conducted to compare growth of Douglas-fir and western hemlock seedlings in 4 soils, with and without forest floor (FF), and with and without fertilizer. Seedlings were 9 months old, and soils of the Klone, Vesta, Bunker, and Shelton series were used. The FF and the fertilizers, ammonium nitrate (100 kg N/ha) and triple superphosphate (226 kg P/ha), were added to the top of the planting pots without mixing. Diameter and height growth, and shoot and root dry weights were determined. With and without fertilizer, growth of both species varied by soil, and seedlings grew mostly better with than without FF. N fertilizer reduced growth of both species in 3 soils, and in some soils, reductions were more with than without FF. P fertilizer improved growth of both species in all soils and with one exception, growth was much greater with than without FF. Results demonstrate importance of FF to nutrition and growth of Douglas-fir and western hemlock, especially when fertilizers are used.

SEED ZONE TEMPERATURE AND MOISTURE CONDITIONS IN A PARTIALLY FROZEN SOIL/CROP RESIDUE SYSTEM. W.R. Bidlake, G.S. Campbell, and R.I. Papendick, USDA-ARS. Washington State University, Pullman.

A mechanistic model was developed to simulate heat and water transport in a partially frozen soil/crop residue system. The model was used to examine effects of two tillage and residue management systems for barley production in interior Alaska, and to explore options for providing favorable seed zone conditions. Field and laboratory experiments were conducted to estimate values for important transport parameters. Simulated soil temperature, soil water matric potential, and depth to frozen soil were compared with measured values for the period of April 19 to June 9, 1986. Simulated and measured soil temperatures and soil water matric potentials indicated that no-till soils are cooler and wetter than conventional-till soils. It is concluded that cool seed zone temperatures under no-till systems may be ameliorated by decreasing planting depth.

W-WAVES AND BIOLOGICAL CLOCKS. O.E. Wagner. Wagner Research Lab., Rogue River, Oregon 97537.

The frequencies of W-wave signals found in plants and animals (observed on a spectrum analyzer) appear, by an experiment that involved placing W-wave signal sources in shields, to be multiples of the earth's rotation frequency (1/86400 Hz). Since plants seem to be dependent on W-waves for growth (e.g. branch and other spacings seem to be determined by standing W-waves and genetics (1)) it appears that plants (and likely animals) through the medium of W-waves have a built in reference for biological clocks. Thus it appears that W-waves not only are involved in the control of plant spacings but likely also in the beating of the human heart. (life frequencies observed so far appear to be multiples of 0.16 Hz which is the 13824th harmonic (multiple) of 1/86400 Hz exactly, not taking into account small solar day length changes; also common higher amplitude W-wave frequencies are multiples of 1.6 Hz)).

(1) O.E. Wagner: Bull. Amer. Phys. Soc. 34:110, 111 (1989).

TOXICITY TESTING USING MICROBIAL SYSTEMS. R.C. Rychert. Boise State Univ., Boise.

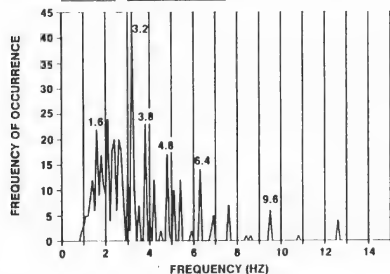
Two assay variations of the Microtox test using *Photobacterium phosphoreum* exhibited no difference with select toxicants except zinc. Inhibition of bioluminescence in *Vibrio fischeri* may also serve as a toxicity bioassay with a sensitivity greater than or equal to the Microtox test. Toxicants have also been shown to lower cellular ATP levels in the unicellular, ciliated protozoan, *Tetrahymena pyriformis*. Cellular ATP levels in the latter were determined with the firefly luciferin/luciferase system and toxicant effects on *T. pyriformis* ATP levels reflected the growth state of the organism. The following toxicants were evaluated in the previously discussed tests: 2,4-dichlorophenoxyacetic acid, sodium pentachlorophenate, sodium dodecyl sulfate, lead, copper and zinc.

PLANT COMMUNICATION AND W-WAVES. O.E. Wagner. Wagner Research Lab., Rogue River, OR 97537.

During March and April 1988 (Bull. Amer. Phys. Soc. 33:2203; 34:110,111) we found that tree damage not only produced voltage changes from probes in the damaged tree but also delayed voltage changes were observed coming from nearby trees. e.g. for trees at 28.6, 13.7, 2.1, 4.9, 14.0, 34.4, 17.6, 35.4, 7.3, 33.2, 5.2, and 31.7 m away from transmitting (ax chopped) trees voltage changes were 0.3, 0.5, 0.1, 0.1, 0.3, 0.2, 0.3, 0.1, 0.1, 0.1, 0.2, and 0.1 mv respectively. The large variations in amplitude are likely due to failure to optimize probe and chop locations to the wave patterns in the trees. These experiments indicated a velocity for W-waves between trees of near 4.8 m/sec. Capacitor sensors in the vicinity of plants continuously indicate W-wave frequencies coming from the space near plants. Direct rather than mediated communication is indicated.

PLANT SPACINGS AND W-WAVES. O.E. Wagner. Wagner Research Lab., Rogue River, OR 97537.

Apparently one of the constraints on a plant spacing is that it conforms to the standing wave pattern in the plant. If a spacing is converted to frequency (Hz) (frequency equals 96 cm/sec divided by twice the spacing) it should fit a measured W-wave frequency. e.g. for 429 branch spacings from the lower branches of five *Pinus ponderosa*:



Peaks match larger amplitude spectrum analyzer measured W-wave frequencies.

ADVERSIVE CONDITIONING WITH THIRAM TO REDUCE MOUNTAIN BEAVER DAMAGE TO DOUGLAS-FIR SEEDLINGS. D.L. Campbell and J. Evans, USDA Animal & Plant Health Inspection Service, Science & Technology, Olympia, WA

Thiram (tetramethylthiuram disulfide, TMTD) has been used extensively in the past as a 10% foliar spray to reduce snowshoe hare (*Lepus americanus*) damage to forest seedlings. This concentration did not appear effective against mountain beavers (*Aplodontia rufa*) when applied to planted seedlings. A recent study of aversive conditioning with a 21% active thiram spray with 23% Rhoplex AC-33 adhesive indicated favorable mountain beaver repellency. The trial was conducted by spraying cull Douglas-fir (*Pseudotsuga menziesii*) seedlings placed in mountain beaver burrows for aversive conditioning. Two-year-old Douglas-fir seedlings averaging 44 cm tall were planted outside each burrow in groups of eight (144 per treatment). Some seedlings were sprayed and others were not. After 8 months, conditioned mountain beavers had cut 17.4% of thiram-sprayed trees and 16.0% of unsprayed trees. On sites where thiram was not applied, 94.4% of untreated control trees were cut outside untreated burrows. Thiram significantly reduced mountain beaver damage.

THE FATE OF DINOSEB (4,6-DINITRO, 2-sec-BUTYL PHENOL) IN SEVERAL IDAHO SOILS VARYING IN SOIL TYPE AND EXPOSURE HISTORY. T.O. Stevens and R.L. Crawford. Dept. of Bacteriology and Biochemistry, University of Idaho

The herbicide dinoseb is found as a soil contaminant at numerous sites in the Northwestern U.S.A. As part of the development of a bioremediation system, we examined the ability of native microorganisms to degrade dinoseb, and the chemical interactions of dinoseb with various Idaho soils from these sites. Degradation rates in silt-loam soils were inversely related to prior dinoseb exposure, indicating that selection for dinoseb-degrading microorganisms had not occurred. Little or no degradation occurred in sandy soils. Reversible and irreversible sorption of dinoseb to soil surfaces was extensive in the silt-loam soils, and was partly pH-dependent. The availability of dinoseb was increased 7-fold by neutralizing the soil pH. Irreversibly sorbed dinoseb could be released by microbiological activity. These factors should be considered when designing a biological treatment system for dinoseb-contaminated soils.

PHYSICAL STRUCTURE, FLORA AND FAUNA OF MOUNTAIN BEAVER NESTS. M.G. Carey, D.L. Campbell, and C.L. Campbell. USDA Animal Plant Health Inspection Service, Olympia WA.

Twenty eight mountain beaver (*Aplodontia rufa*) nests in a 1-yr old burned and planted clear-cut were excavated and examined. Physical measurements taken included depth below ground and size of nest cavity. Nest material was collected from eight nests and sorted into vegetation types. Arthropods were collected from nest material by visual search and Berlese funnel. Depths of mountain beaver nests averaged 74 cm, ranging from 30 to 183 cm. Nest chambers were roughly egg shaped, averaging 51 cm long, 43 cm high and 43 cm wide; chambers usually had one entrance. Available plants were still sparse since slash burning. Nests consisted of the most common plants available that were not utilized as food, such as groundsel (*Senecio* sp.), horsetails (*Equisetum* sp.), thistle (*Cirsium* spp.) and mosses. Arthropods were primarily mountain beaver fleas (*Hystrichopsylla schefferi*), pseudoscorpions, mites and at least 3 families of beetles (Staphylinidae, Scarabaeidae, and Histeridae).

THE EFFECT OF BEAVER ON STREAM AND STREAM-SIDE CHARACTERISTICS AND COHO POPULATIONS IN WESTERN OREGON. K.L. LEIDHOLT, W. McCOMB and D.E. HIBBS. Oregon State University, Corvallis

The focus of this study was the effect of beaver (*Castor canadensis*) on two coastal Oregon stream systems. Analysis of food preferences shows that beaver have the highest preference for 2-9 cm alder and salmonberry. Salmonberry appeared to be most important in April-June; later, alder and herbaceous vegetation were more important. Most foraging was within 30 m of the stream. Discriminate function analysis (DFA) showed that proximity to a tributary, logjam, or debris slide had the strongest positive effects on beaver habitat suitability; vegetation characteristics added little explanatory power. Beaver dams increased the amount of pool habitat available to coho salmon, especially in late summer. Beaver also provide extra coho rearing habitat, especially in late summer during reduced water flow. In heavily managed streams, beaver may be able to provide structure and stability, at a much lower cost than stream rehabilitation projects.

METHODS FOR RELOCATION OF PREY FOR NORTHWEST RATTLESNAKE, CROTALUS VIRIDIS OREGANUS, Bill Robinson and K. V. Kardong, Washington State University, Pullman, WA 99164-4220.

After the initial strike and envenomation of Crotalus viridis oregonus, the prey (adult Swiss Webster) flees and soon dies. Now following a scent trail the rattlesnake starts its search to recover the prey. The purpose of this experiment was to determine the factors involved in this relocation process. Rattlesnakes were introduced to a maze of scent trails, which ran sixty centimeters straight out of the snake cage and then split. Thus, as the snake followed its victim's trail a decision had to be made once the division point of the scent trail was reached. Different variations of scent trails were used including the scent of the individual mouse, a venom reaction in the mouse, a trauma reaction in the mouse, or the heat of the trail. It has become clear that the snake is using a combination of these factors. A hierarchy of these strategies is presently being addressed.

MICROHABITAT SELECTION BY MICROTUS MONTANUS: FEMALE CHOICE. M.A. O'Connell and J.G. Hallett. Washington State University, Pullman, WA.

The polygynous mating systems of most mammals suggest that habitat selection by females should be dictated by resource quality to ensure successful reproduction. In contrast, habitat selection by males should reflect female distribution. We examined microhabitat selection by Microtus montanus during colonization of an unoccupied habitat. Voles have been monitored by live trapping since spring 1986 on a 1 ha grid in the shrub-steppe of eastern Washington. Microhabitats were identified by performing principal components analysis on vegetational characteristics measured at each of the 100 grid stations. In the first phase of colonization, voles exhibited definite microhabitat preferences. With increasing density, peripheral microhabitats were entered hierarchically with males preceding females. At peak density, sex ratios in all microhabitats were equal.

HIERARCHICAL CLUSTER ANALYSIS AS AN AID FOR INTERPRETING HERBIVORE DIETS. M.L. McInnis, L.L. Larson and M. Vavra. Oregon State Univ., Corvallis.

Hierarchical cluster analysis has received little attention in food-habits research. Clustering similar samples is especially useful in eliciting internal structure of large data sets (two-way matrices of at least 10 by 10) and can provide insights into feeding strategies and competition among animals. As an example, we classified seasonal diets of 3 species of sympatric herbivores using complete linkage clustering. The resulting dendrogram allowed us to correctly classify herbivores as grass-consumers (feral horses and domestic cattle), or forb- and shrub-consumers (pronghorn). The analysis further showed horses and cattle consumed diets most similar during spring and summer and least similar during fall and winter. The dendrogram clearly revealed pronghorn switched from a shrub-dominated diet during fall and winter to a diet composed principally of grasses and forbs in summer.

TIMING AND LOCATION OF ALGAL HOST USE BY AN OLIGOPHAGOUS MARINE HERBIVORE. C.D. Trowbridge. Oregon State Univ., Corvallis.

Larval recruitment of the sea slug Placida dendritica to its green algal hosts was continuous during the spring and summer at four sites along the central coast of Oregon. Because Placida had an extremely short life span, Placida populations were composed of many overlapping generations. Placida aggregated in depressions on the rugose, crustose alga Codium setchellii and in the axillary region of branches on the upright alga C. fragile. Placida's grazing results in fragmentation of C. setchellii and branch loss in C. fragile. The timing of Placida recruitment coupled with the location of grazing indicate that the herbivore may have important effects on the survival of its algal host.

PLATYRRINE SPECIES DISTRIBUTION AND THE THEORY OF CORROBORATING EVIDENCE. L. E. Mackelburg, and R.W. Thorington, Jr. Wash State Univ.; Smithsonian Institution, Washington, DC.

The theory of corroborating evidence is basic to determining species distributions. Range boundaries are drawn between areas where it has been collected and areas where it has not and is assumed not to occur. Intensity of collecting effort isn't usually considered, e.g., all collecting localities of Saguinus midus niger occur south of the Rio Amazonas, between the Rios Xingu and Guriup (Hershkovitz, 1977). It is assumed that the Rio Xingu is the western boundary for this primate, but within its known range it has been taken at only 19 of 75 collecting localities. Thus there is a 75% chance that it will not be collected at any one collecting locality. Within 2° west of the Rio Xingu, there are only 9 primate collecting localities. Thus the probability that it occurs there but has not yet been collected is $(.75)^9$ or 7.2%. The Rio Xingu as the western boundary of S. m. niger is only weakly corroborated. This analysis has proven to be a useful tool in examining species distributions, and may be extended to other hypotheses.

THYROXINE AND INDUCED METAMORPHOSIS IN OVERWINTERING TADPOLES OF THE TAILED FROG, ASCAPHUS TRUEI. H. Brown. Western Washington University, Bellingham.

Tadpoles were collected from montane streams near Mt. Baker during September and October and maintained in different concentrations of thyroxine at several temperatures. Morphological changes in mouthparts, body size, size of tail, spiracle, anal fold, and forelimb and hindlimb were measured. No changes occur when reared at 5 C. There are great changes in most features, except mouthparts and tail, when reared at 10 or 20 C. Tadpoles of one and two years age are less sensitive than three year tadpoles. Low temperatures of streams probably inhibit larval development and differentiation, and this results in a four year larval period.

METEOROLOGICAL AND HYDROLOGICAL DROUGHT IN WASHINGTON STATE, 1986-88. R. Quinn. Eastern Washington University.

The 1986-88 drought in Washington State was characterized by winter deficiencies in precipitation of 70 to 90 percent in most climatic divisions. Hydrologically dependent resources such as hydropower, fisheries, recreation, and forestry were heavily affected. Palmer drought indexes became negative in 1985 in most climatic divisions and reached moderate to extreme values by the fall of 1987. The 1986-88 drought was accompanied by a moderately strong ENSO event and large positive 700 millibar height departures over western Canada and the Pacific Northwest. Similar height patterns were observed in the droughts of 1972-73 and 1976-77.

DEVILS KITCHEN THERMAL AREA AT MOUNT HOOD, OREGON, REVISITED. K.A. Cameron, U. S. Geological Survey, Cascades Volcano Observatory, Vancouver, WA

The Devils Kitchen thermal area, located on the terminal moraine of Coalman Glacier, was revisited during October 1988, the same time of year as the original survey completed in 1987. During the original survey topographic and thermal contour maps were made of the area. Another thermal map was completed this year, allowing direct comparison of the thermal structure of the field in succeeding years. Major fumarole vent locations and temperatures were, for the most part, unchanged. Temperatures were near local boiling (194° F) with a few superheated by up to 4° F. Ground temperatures had risen markedly, although the heat pattern remained the same. Temperatures near the center of the thermal area averaged 20° F higher than in 1987. This may be due in part to the disappearance of a small lake which usually occupies the area between the glacier snout and the moraine. This lake, which apparently drained from the bottom, may have had a tempering effect on heat flow through ground-water seepage. No cause could be found for the disappearance of the lake.

ELECTRON TRANSFER AND RADICAL CATION REACTION RATES OF METHOXYLATED BIBENZYL. G. E. Fryxell, M. Chow, W. A. Rodin and D. M. Camaioni. Battelle, Pacific NW Laboratories, Richland, WA.

Arene radical cations have received a great deal of attention recently. In order to develop practical methods to employ these unique reactive intermediates, we have sought a detailed mechanistic portrait of the pathways available to these open shell species. One of our approaches has involved measuring the kinetics of base promoted tris(phenanthroline) iron(III) oxidation of substituted alkylarenes. Rate data thus far obtained for methoxylated bibenzyls and related compounds provide insight into C-C bond cleavage, C-H bond cleavage and the facility of pi-pi overlap between the two arene rings. The results for these compounds will be presented in a structure/reactivity framework to emphasize the influence of substrate structure on the various reaction pathways.

REINTERPRETATION OF THE ALPINE GLACIAL SEQUENCE IN THE LEAVENWORTH AREA, WASHINGTON W.A. Long, 123 Riverfront Dr., Cashmere, WA 98815

Long and Porter (1968) distinguished three major Pleistocene drift sheets in the Leavenworth area on the basis of preservation of moraines, weathering of granite boulders, and soil development. The youngest drift (Leavenworth) has been further subdivided into four glacial advances on the basis of moraines in lower valley sections. Glacier Peak tephra (11,250 yr B.P.) on some valley-head moraines shows a probable post-Leavenworth IV advance. The only known deposit of oldest drift (Peshastin) is an extensively weathered lateral moraine on the high southern crest of Boundary Butte Ridge. Distribution of intermediate drift (Chumstick) along the northernmost 1.5 miles of Boundary Butte Ridge and in adjacent Wenatchee Valley shows that the glacier overtopped this part of the ridge and reached Dryden. A terminal moraine at the mouth of Chumstick Creek represents a recession or readvance from the Chumstick maximum. Thick, deeply weathered boulder gravels that had been interpreted as Peshastin drift rest on Eocene strata in Wenatchee Valley below Leavenworth. Because granite boulders in the gravel and in Chumstick moraines show uniform weathering that has resulted in grus-surrounded solid cores, in marked contrast to the largest Peshastin granitics which have no residual cores, the boulder gravel is believed to be Chumstick in age. Chumstick terminal zone drift underlies bedded sand and silt containing unweathered granite dropstones which, during the Leavenworth maximum, were ice-raftered downvalley into a lake ponded to at least 1100 feet altitude by a landslide in Columbia Valley.

VIVIANITE FROM KALALOECH, OLYMPIC PENINSULA, WASHINGTON. S.R. Benham, Fred L. Tobiasson, and M.J. Thielman. Pacific Lutheran University, Tacoma, WA.

Vivianite $\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$ collected from conifer tree roots, trunk wood and authigenic nodules preserved in several Pleistocene peat bogs exposed in sea cliffs north of Kalaloech was analyzed using FTIR and ICP. Cation substitution for iron is very low. Ca^{2+} ranges from 20-260ppm and Mg^{2+} ranges from 10-500ppm. Iron composes 29.8-41.0% of vivianite from these deposits. Sample composition is independent of the mineral color and texture, which ranges from tan rinds to chalky vivid blue infillings in wood and nodules. Macroremains and pollen data indicate the vivianite is associated with peat deposits that accumulated in a cool, temperate interglacial period or in front of a glacial advance more than 70,000 radiocarbon years ago.

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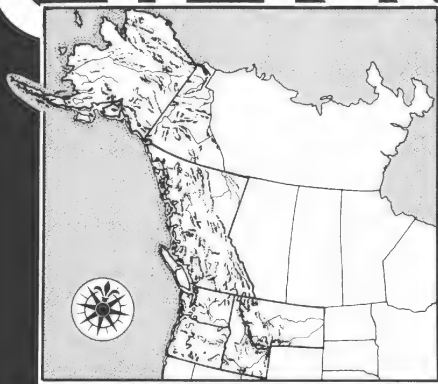
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NORTHWEST SCIENCE

Tree Communication?



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Announcements

In This Issue

Five or six years ago, several researchers discovered what seemed to be communication between plants. A tree under stress, as by insect attack, apparently communicated this to surrounding trees which in turn produced secondary chemicals within their tissues that discouraged insect attack upon themselves. The popular press could not resist, and unfortunately this became known as the "talking trees" phenomenon.

Yet, some evidence does exist that trees can mutually influence each other, "communicate." The first guesses as to the agent of communication was a pheromone, a chemical released by the attacked tree and carried by wind to surrounding trees. Several years ago, Dr. O. E. Wagner, physicist by training, began experiments that led him into this subject and suggests an alternative medium by which trees communicate. Although still tentative, his ideas are intriguing. His article appears in this issue.

Meeting of Interest

Regrettably, this meeting announcement reached the editor much too late to include in an earlier issue, but for general information is mentioned: Wilderness/Parks Fire Conference: Fire policies & management strategies in Wilderness & Parks—Past & Future, held in Bozeman, Montana 23-26 May 1989. For questions on technical content contact Paul Weingart, co-chair, 108 Circle Drive, Bozeman, MT 59715, or Jim Saveland, co-chair, Southern Forest Fire Laboratory, Rt. 1, Box 182-A, Dry Branch, GA 31020.

In Memoriam

Charles Duncan Campbell, Emeritus Professor of Geology, Washington State University, died on December 10, 1988, at his home in Carmel, California, after a lengthy illness. He is survived by his widow, Dorothy, in Tucson, Arizona.

Charles was born in 1905 at Ann Arbor, Michigan, the son of Jennie Campbell and Edward D. Campbell, Professor of Chemistry at the University of Michigan. He earned his B.S. and M.S. degrees at the University of Michigan and a Ph.D. degree in 1934 at Stanford University. He joined the WSU Geology Faculty the same year where he taught until his retirement in 1971. He served as Chairman of the Department of Geology from 1950 to 1961.

His teaching of undergraduate and graduate classes in petrology, petrography, mineralogy, and general geology was marked by thoroughness and clarity, enlivened by his keen wit. Field work during his teaching years included geologic mapping in Washington State for the State Division of Mines and Geology and for the United States Geological Survey.

Charles was a Fellow of the Geological Society of America and the Mineralogical Society of America and a member of several other professional societies including the Northwest Scientific Association. He served as Vice-President (1959-1960) and President (1960-1961) of the National Association of Geology Teachers. He authorized some dozen and a half papers, mostly in petrology and petrography, in publications of the United States Geological Survey, *American Journal of Science*, *Geological Society of America*, *American Mineralogist*, *Journal of Geophysical Research*, *Journal of Geological Education*, and *Northwest Science*.

The Department of Geology, Washington State University, is establishing a Charles D. Campbell Endowment Fund supported by present and former faculty, students, staff, and friends who benefited from and greatly enjoyed their association with him.

—Joseph W. Mills

Early Summer Diet and Food Preferences of Northern Pocket Gophers in North Central Oregon

Abstract

Studies of food habits and food plant preferences of the northern pocket gopher, *Thomomys talpoides*, were conducted in a Mima-mound habitat at the Lawrence Memorial Grassland Preserve, north-central Oregon, in early June, 1987. Stomach contents of 15 pocket gophers trapped in early June showed a predominance of forb shoots, particularly those of *Lupinus*, although roots dominated in two individuals, and were present in small amounts in most individuals. Preferences were determined by in-tunnel, cafeteria-style tests. Pocket gophers showed strong preferences for several plant species that were limited to the inter-mound scabland or stone bed habitats. Strong preference was also shown for certain mound species, such as *Lupinus caudatus*. These observations, together with those of other workers, indicate that members of the genus *Thomomys* feed primarily on herbaceous shoots, especially in summer, and that forb shoots are often much more heavily used than the shoots of grasses.

Introduction

Large areas of the Columbia Plateau are covered by Mima-mounded scabland where the mounds commonly attain heights of 2 m, diameters of 20 m, and densities of 25 ha⁻¹. Thin lithosols cover the basaltic bedrock of the intervening scablands. The mounds and neighboring scablands differ markedly in vegetation. Deeper silt loam soils of the mounds are dominated by grassland species such as *Agropyron spicatum* and *Festuca idahoensis*, whereas the shallow scabland soils are dominated by an *Artemisia rigida*-*Poa secunda* association (Daubenmire 1970, Winward and Youtie 1978).

Investigations of Mima mounds at the Lawrence Memorial Grassland Preserve, near Shaniko, north-central Oregon, support the hypothesis that the mounds are formed by gradual translocation of soil by the northern pocket gopher, *Thomomys talpoides*, toward the deep, well-drained microsites where these animals center their activity (Cox *et al.* 1987). Translocation results from the backward displacement that accompanies outward tunneling from centers of activity. By mining soil from intermound areas, this translocation also contributes to the formation and maintenance of the intermound scablands.

It has been hypothesized that mining of soil by pocket gophers creates the sharply defined beds of sorted stones that encircle many mounds and form polygonal nets in intermound areas at many locations on the Columbia Plateau (Cox and Allen 1987). Formation of these beds may

result from the collapse of tunnels dug beneath them by animals in search of certain highly preferred food plants. These beds possess a distinctive flora of geophytic perennials (Daubenmire 1970, Winward and Youtie 1978) that may be restricted to this microhabitat by intense pocket gopher herbivory.

These observations suggest that the pocket gopher has a significant effect on the grassland ecosystems of the Columbia Plateau through control of the composition of vegetation. The present study was undertaken to obtain information on food plant preferences and use patterns, and on how these patterns relate to the distribution of plants in the mound-intermound habitat mosaic.

Methods

Studies were conducted at the Lawrence Memorial Grassland Preserve (LMGP) and on adjacent ranch land of the Priday Brothers Corporation, Wasco County, Oregon (44°57'N, 120°48'W), in June, 1987. The LMGP is a Registered National Landmark owned by the Nature Conservancy. It lies at an elevation of 1036-1060 m on the Shaniko Plateau (formed of Columbia River basalts) and includes within it several ravines that fall steeply northward into the valley of Ward Creek, 122 m below. The preserve has a cold semi-desert climate, with an average annual precipitation of 280 mm. The surface of the plateau is mounded "biscuit scabland" with Mima mounds that range up to about 1 m in height and 20 m in diameter. Mound soils are Condon eolian silt loams, whereas the intermound soils are residual

Bakeoven loams. The vegetation of mounds and deeper upland soils is dominated by Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Agropyron spicatum*). The shallow intermound soils are dominated by scabland sagebrush (*Artemisia rigida*), Sandberg bluegrass (*Poa scabrella*), several species of biscuitroot (*Lomatium* spp.), and bitterroot (*Lewisia rediviva*). The northern pocket gopher is abundant throughout the preserve. A comprehensive physical and biotic inventory of the LMGP is given by Copeland (1980).

Pocket gophers were trapped on ranch land adjacent to the southern and western boundaries of the LMGP to obtain material for stomach contents analysis. Sex, age, reproductive status, and weight were recorded for all animals captured. Stomachs were removed and preserved in 70% ethanol for dietary analysis.

Stomach contents were analyzed at the Composition Analysis Laboratory, Colorado State University, using the microhistological analysis techniques outlined by Sparks and Malechek (1968) and Dearden *et al.* (1975). The analyses were based on examination of 20 fields on each of the three slides made from each stomach sample.

Data on preferences for leaves, stems, and belowground parts of 14 predominant plant species of the mound-and-scabland habitat were obtained by a series of in-tunnel, cafeteria-type preference tests. Species recognized as dominants of mounds and intermound scabland by Winward and Youtie (1978) were chosen for testing. Tunnels of pocket gophers were located with a metal probe. On one side of the tunnel, an alcove about 6 cm wide and 12 cm long was dug. Three food items, each cut or bundled to form a 10-g unit, were positioned in this alcove so that they did not impede passage of an animal through the tunnel. The tuber of biscuitroot, *Lomatium cous*, a preferred food, was used in each test to serve as a standard against which to compare preferences for other species. *L. cous* is almost completely restricted to intermound stone beds that pocket gophers penetrate only with difficulty (Cox and Allen 1987). The sequence of the three items was varied systematically from one tunnel to another in test replicates. An effort was made to obtain at least 10 positive preference tests (tests in which one or more items was removed) for each combination of items.

Preferences were evaluated using Fisher's Exact Test (Zar 1974). Plant names follow Hitchcock and Cronquist (1973).

Results

The stomach contents of 15 animals consisted primarily of plant root and shoot material, with seeds and arthropod fragments also present in minute amounts (Table 1). Root material averaged 20.7 percent and shoot material 79.1 percent of the stomach contents. Root material ranged from 0 to 100 percent of individual stomach contents, but in only two cases did roots constitute over 50 percent of the material present.

Grasses constituted 2.4 percent, and forbs constituted 97.0 percent of the shoot matter eaten. Lupine, probably all *Lupinus caudatus*, averaged 70.9 percent of the shoot matter consumed. In six of the ten stomachs of adult animals more than 70 percent of the material present was lupine. Buckwheat, probably all *Eriogonum heracleoides*, and yarrow, *Achillea millefolium*, were other mound dominants that were taken in significant amounts.

Evidence of plant harvesting was also obtained incidental to the preference tests. Sections of cut petioles and stems of *Lupinus caudatus*, 2-5 cm long, were encountered frequently in the loose soil on tunnel floors and in the soil used by animals to plug tunnel sections. *Lupinus caudatus* leaves were also occasionally found in tunnels, as well as small quantities of fine grass roots, seeds of cheat grass, *Bromus tectorum*, and leaves of *Trifolium macrocephalum*.

Fourteen plant species were used in the in-tunnel preference tests (Table 2). For plant species dominant on the mounds, high preferences (not significantly different from those for *L. cous*) were noted for roots of *Lomatium triternatum* and *Achillea millefolium*, and for leaves of *Lupinus caudatus*. For the remaining seven items, preferences were weaker. Among species dominant in the intermound zone, which included the beds of sorted stones, high preferences were noted for rootstocks of *Lomatium minus*, leaves of *Trifolium macrocephalum*, and bulbs of *Allium tolmiei*.

Intermound food items were taken more often than mound items. This difference is strongly significant, even when the total number taken for *L. cous* is considered to be 10 (the integer nearest

TABLE 1. Diets of 15 northern pocket gophers collected at the Lawrence Memorial Grassland Preserve, north-central Oregon, 3-6 June 1987, expressed as percent composition of stomach contents by dry weight (see text for details).

Component	Number of Stomachs	Mean Percent Composition	Range in Occupied Stomachs (Percent)
ROOTS/CORMS			
Roots	12	20.6	0.5-100.0
Corms	1	0.1	1.2
SHOOTS			
Grasses			
<i>Agropyron</i>	1	0.7	10.1
<i>Aristida</i>	1	0.1	1.0
<i>Bromus</i>	2	0.2	1.2-1.3
<i>Festuca</i>	6	1.2	0.5-11.2
<i>Poa</i>	2	0.2	1.2-1.6
Forbs			
<i>Achillea</i>	6	4.6	1.6-43.6
<i>Calochortus</i>	1	0.2	2.3
Compositae	1	1.3	19.6
<i>Eriogonum</i>	2	12.5	92.2-95.0
<i>Erodium</i>	1	0.1	2.1
<i>Lupinus</i>	11	56.1	10.0-100.0
<i>Penstemon</i>	1	0.1	1.1
<i>Ranunculus</i>	1	1.0	15.5
Flowers	5	0.8	0.6-4.8
Seeds	3	0.2	0.5-1.7
ARTHROPODS	1	0.2	1.4
TOTAL		100.2	

the mean value for this species in the eight series of tests) (Contingency $\chi^2 = 8.30$, DF = 1, $P < 0.01$). Segregating items as aboveground or belowground parts showed no significant preference by pocket gophers (Contingency $\chi^2 = 3.28$, DF = 1, $P > 0.05$).

Discussion

Stomach contents data from LMGP indicate that the early summer diet of pocket gophers consists mostly of forb shoots. Data from studies of *Thomomys* pocket gophers in the western United States show a strong tendency for shoot material to constitute most of the annual diet. In south-central Oregon, Burton and Black (1978) found that shoot material made up most of the diet of *T. mazama* in every month except March. On Black Mesa, Colorado, Ward and Keith (1962) found that the consumption of shoot material by *T. talpoides* was 69.4-79.4 percent from June to September, with root consumption rising to 61.8 percent in October. Ward (1960) observed a

strong seasonal cycle in the representation of root and shoot material in the diet of *T. talpoides* living in mixed grass and alfalfa fields near Livermore, Colorado; there over 90 percent of the diet consisted of shoots in June, and over 90 percent of roots from December through March. Vaughan (1967) likewise noted that shoots constituted 76 percent of the summer diet of *T. talpoides* in Weld County, Colorado but only 61 percent of the winter diet. In Grand County, Colorado, Vaughan (1974) found that shoot material constituted 90 percent of the summer diet of *T. talpoides*. Criddle (1930) noted that green foods, especially legumes and *Artemisia*, were preferred by *T. talpoides* during summer in Manitoba. Ingles (1952), however, concluded that the summer diet of *T. monticola* in the Sierra Nevada Mountains of California consisted mostly of roots, and the winter diet mostly of shoots, which were harvested in snow tunnels on the ground surface.

Foods of *Thomomys*, especially in fall and winter, are often stored as caches in underground

TABLE 2. Results of preference tests conducted in tunnels of the northern pocket gopher at the Lawrence Memorial Grassland Preserve, north-central Oregon, with plant materials of dominant mound and intermound species.

	Number of Tests	Taken	Partially Taken	Not Taken	Fisher's Exact Test
<i>Mound Species</i>					
<i>Lomatium triternatum</i> taproot	9	9	0	0	ns
<i>Lupinus caudatus</i> stems	13	6	1	6	P < 0.01
<i>Lupinus caudatus</i> leaves	9	9	0	0	ns
<i>Festuca idahoensis</i> roots	12	3	0	9	P < 0.001
<i>Agropyron spicatum</i> roots	10	1	0	9	P < 0.001
<i>Bromus tectorum</i> seed heads	9	1	1	7	P < 0.001
<i>Eriogonum heracleoides</i> leaves	9	2	0	7	P < 0.01
<i>Chrysothamnus viscidiflorus</i> leaves	10	4	0	6	P < 0.01
<i>Achillea millefolium</i> stems + leaves	12	8	1	3	P < 0.05
<i>Achillea millefolium</i> roots	10	7	0	3	ns
Total	103	50	3	50	
<i>Intermound Species</i>					
<i>Lomatium cous</i> tuber	82	82	0	0	—
<i>Lomatium minus</i> rootstalk	9	9	0	0	ns
<i>Allium tolmiei</i> bulbs	10	9	0	1	ns
<i>Trifolium macrocephalum</i> leaves	10	9	0	1	ns
<i>Sitanion hystrix</i> shoots, seed heads	10	3	0	7	P < 0.01
<i>Artemisia rigida</i> leaves	13	9	1	3	P < 0.05
Total	134	121		12	
GRAND TOTAL	237	171	4	62	

chambers or chambers in snowbanks (Criddle 1930, Aldous 1945, Tryon 1947, Ingles 1952, Ward 1977, Stuebe and Andersen 1985). Roots, corms, and bulbs predominate in most of these caches, although seeds (Criddle 1930, Aldous 1945) or leaves of shrubs (Ingles 1952) or herbs (Ward 1977) are sometimes the primary materials. *Thomomys* species also tend to feed more heavily on woody plants during winter (Burton and Black 1978, Gettinger 1984). Stuebe and Andersen (1985) noted that the items stored in greatest amounts tended to be those low in nitrogen content, such as the roots of *Orogenia linearifolia* and *Claytonia lanceolata*.

The representation of grasses in the LMGP sample is much lower than that observed in most other studies of *Thomomys* diets. Large quantities of grasses are consumed by *Thomomys* pocket gophers in some areas, but different species are often utilized in a highly seasonal manner. Vaughan (1967), for example, noted that *Stipa comata* was used heavily from December through May, whereas *Agropyron smithii* was used heavily

ly from May through September, and *Bouteloua gracilis* was consumed in substantial amounts only in June. Aldous (1951), who estimated summer shoot harvest from evidence of plant cutting near tunnel openings, found that *T. talpoides* in mountain meadows in Utah harvested only 18.2 percent grasses, as opposed to 81.8 percent forbs. Vaughan (1974) noted that 91.7 percent of the shoot material consumed by *T. talpoides* in Colorado mountain meadows consisted of forbs.

In most cases, grasses alone do not seem to provide an adequate diet for *Thomomys* species. On Grand Mesa, Colorado, where 2,4-D treatments were used to reduce the abundance of weedy forbs and favor grasses, Keith *et al.* (1959) noted a strong shift by *T. talpoides* from a predominance of forbs to one of grasses in the diet. However, the pocket gopher population showed a decline of 87 percent on the sprayed areas. Studies by Tietjen *et al.* (1967) on Black Mesa, Colorado, showed that after 2,4-D spraying pocket gopher populations were reduced 80-90 percent, roughly proportional to the decrease

in forb abundance. In addition, they showed through feeding experiments that only use of certain succulent, rhizomatous or cormose grasses enabled animals to maintain body weight. The dominant grasses of mound habitats at the LMGP (*Agropyron spicatum* and *Festuca idahoensis*) lack these characteristics. Nevertheless, at certain times of the year, roots of these grasses may be important foods. In September 1985, for example, plants of *Agropyron spicatum* were observed at LMGP with the entire root systems consumed by pocket gophers (D. B. Lawrence, pers. comm.)

The heavy feeding on *Lupinus* noted in the LMGP sample has been observed by other workers. Vaughan (1974) noted that 48.9 percent of the summer diet of *T. talpoides* in Colorado mountain meadows was *Lupinus argenteus*. Ward and Keith (1962) found that on Black Mesa, Colorado, *Lupinus* spp. made up about 15.2 percent of the diet of *T. talpoides* and that plants of this genus were among the most highly preferred food items, based on their representation in the diet relative to that in the vegetation. Keith *et al.* (1959) also noted that *Lupinus* was a main food item of *T. talpoides* on Grand Mesa, Colorado, and Aldous (1951) found it a common food in central Utah. *Lupinus* is consumed by *T. talpoides* in both Utah and Washington (D.C. Andersen pers. comm.). Gettinger (1984) found *Lupinus* a small, but consistent, component of the diet of *T. bottae* in southern California.

Preferences, as revealed by in-tunnel tests, may indicate only patterns of differential acceptability of items encountered. At the LMGP, pocket gophers showed strong preference for the roots or tubers of *Lomatium* species. Strong preference was noted for *Achillea* shoots and moderately strong preferences for *Achillea* roots. *Achillea* plant tops killed by pocket gopher harvesting of root systems were also noted by D. B. Lawrence (pers. comm.) at LMGP. Thus, some of the unidentified root material in stomach contents was likely *Achillea* roots, since this species grows abundantly on many mounds at LMGP. Andersen and MacMahon (1981), in contrast, found roots of *A. millefolium* to be consistently avoided. The high preference for roots of *Lomatium* spp. suggests that another component of the unidentified root material in the stomachs consisted of *L. triternatum* taproots. Although preference for these roots was strong,

only 2 of 15 animals showed a preponderance of root material in their stomach contents.

Strong differences in root form exist among the three species of *Lomatium* used in preference studies. *Lomatium cous*, which is largely restricted to the intermound stone bed habitat, has a large, compact tuber that is rooted on the surface of the soil at the base of the zone of bare stones. *L. minus*, almost completely restricted to the stone bed habitat, has a thick, branched rootstock that is typically more massive than that of *L. cous*, and it, too, is rooted at the surface of the soil zone in the stone beds. *L. triternatum*, which is restricted to the mounds, possesses a slender, elongate tap root. The nature of the root systems of *L. cous* and *L. minus* is probably essential to their ability to occupy the stone bed microhabitat, but should not prevent their occupation of the mounds. I hypothesize that pocket gopher herbivory is the cause of this restriction. The slender taproot of *L. triternatum* is probably incompatible with growth in the stone bed habitat, thus restricting it to mound soils. The high preference of pocket gophers for this species, however, suggests that it enjoys some form of protection. Many of the *L. triternatum* plants were rooted in large clumps of *Agropyron spicatum* or *Festuca idahoensis*; the dense root masses of these grasses may protect the *L. triternatum* roots embedded in these clumps.

Strong preferences of pocket gophers for *Allium tolmei* bulbs and *Trifolium macrocephalum* leaves may also limit these species to the intermound scabland soils that are less accessible to pocket gophers. These species are largely confined to areas of scabland at a considerable distance from mound edges. Thus, these species may escape herbivory only by growing far from centers of pocket gopher activity.

The leaves of *Lupinus caudatus* were highly preferred by pocket gophers. This preference was unsuspected until testing. The short stem sections of lupine that were commonly found in the soil of plugged tunnel openings and scattered along the interior of tunnels during our studies suggested that the stems of lupine were being harvested. The tests, however, showed a relatively weak preference for stems. It appears that the stems of lupine are clipped at the base, pulled into the tunnel, and the leaves eaten or cached. The stems are then cut into short sections, perhaps simply to facilitate disposal. This

suggests that material found casually along tunnels may not be used as food. Aldous (1951), noting similar behavior by *T. talpoides* in Utah, concluded that animals were probably consuming the leaves and tender ends of lupine stems and discarding the tougher stem sections.

These observations suggest that knowledge of the diet of animals may be inadequate to reveal the full impact of the feeding activity of these animals on vegetational composition in a heterogeneous habitat such as Columbia Plateau mounded scabland. Some plants that were abundant on mounds were nevertheless major items in the pocket gopher diet. Strong preferences for intermound species, evident only in preference tests, suggested that several species of corm, bulb, or fleshy-rooted perennials that are rare

on mounds are limited to intermound areas by intense herbivory.

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Diets of Wolves on Northern Vancouver Island

Abstract

The purpose of our study was to determine the occurrence and seasonal variation of prey species in the diets of wolves on northern Vancouver Island. Columbian black-tailed deer were found to be the most frequent prey and comprised the greatest relative weight in the diet of wolves. Roosevelt elk comprised the next greatest component by relative weight in the diet. Hairs of fawns occurred with greater frequency in summer scats than did those of adult deer. Beaver hair was more frequent in winter scats than in summer scats. The proportion of beaver in the diet varied among years and was greatest when deer populations were low. On Vancouver Island, young ungulates were important prey of wolves during summer. Use of alternative prey by wolves increased when deer abundance was low.

Introduction

Diets of wolves (*Canis lupus*) are important to understanding their predator-prey relationships. Throughout North America ungulates are the primary prey of wolves (Theberge *et al.* 1978, Scott and Shackleton 1980, Fritts and Mech 1981, and Carbyn 1983). Other species, particularly beaver (*Castor canadensis*), may be seasonally important in the diet of wolves or important during declines in availability of ungulates (Pimlott 1967, Voight *et al.* 1976, Theberge *et al.* 1978).

Our study describes the diets of wolves on northern Vancouver Island. Our objectives were to determine the wolves' major food types, the relative occurrence of these types in their diet, seasonal variation in prey species and age-class utilization.

Study Area and Methods

The study area consists of the Nimpkish River Valley and Adam River Valley on northeast Vancouver Island, British Columbia. The area ranges in elevation from sea level to 2,158 m. Three biogeoclimatic zones occur: the Subalpine-Mountain Hemlock, Coastal Western Hemlock, and Coastal Douglas-fir Zones (Krajina 1965) in a mixture of old-growth forest and cutovers. The area supports two ungulate species, Columbia black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*). Red squirrel (*Tamiasciurus hudsonicus*), beaver, black bear (*Ursus americanus*),

and cougar (*Felis concolor*) also occur in the area.

Wolf scats were collected monthly from transects along secondary logging roads. Collection occurred in the Nimpkish area from March 1983 to October 1985, and in the Adam area from November 1983 to September 1985. Scats were analysed using techniques described by Kennedy and Carbyn (1981). Impressions of guard hairs were examined microscopically for medulla form and cuticular scale pattern. Hair samples were identified using a reference collection of hairs from known species, and a guide to cuticular hair scales (Moore *et al.* 1974). Scats were grouped seasonally based on whether hairs from fawns and calves could or could not be distinguished from those of adults. Summer was June to August and winter included all other months. Hairs of fawns and calves were identified in scats collected from June to August. Maximum diameter, length, and colouration of hair were used to distinguish the hair of fawn deer and calf elk from those of adults (Scott and Shackleton 1980). Hairs of young ungulates (< 1 year old) could not be distinguished from hairs of adults in scats collected from September to May.

Contents of scats were analyzed by determining percent occurrence of prey species in scats and relative weight of each species consumed using the equation proposed by Floyd *et al.* (1978): $Y = 0.38 + 0.02 X$, where Y is kg of prey per collectable scat and X is prey weight (kg). Weights of prey used in our analyses were: adult

black-tailed deer (64.6 kg), fawn black-tailed deer (5.0 kg) (Harestad pers. comm.); adult Roosevelt elk (234 kg) (Bryant and Maser 1982); calf elk (25 kg), beaver (20 kg) (Cowan and Guiget 1965); red squirrel (0.19 kg) (Banfield 1974). Data were analyzed using G-tests (maximum likelihood ratio test) (MYSTAT 1988).

Results

Six hundred and forty seven scats were collected in the two study areas between 1983 and 1985. The prey species were black-tailed deer, beaver, Roosevelt elk, and red squirrel (Figure 1). In scats collected from the Adam area, black-tailed deer occurred most frequently in all years followed by beaver, with the exception of 1985 when elk occurred with a frequency greater than that for beaver. Black-tailed deer was also the most frequent prey species in scats from the Nimpkish area. Elk occurred with the next greatest frequencies, except in 1984 when beaver hair occurred with a frequency of 40 percent compared to 19 percent for elk. Red squirrel occurred least frequently in both study areas for all years.

In terms of relative weight, black-tailed deer was the most important prey species in the Adam area (Figure 1). Black-tailed deer was also the

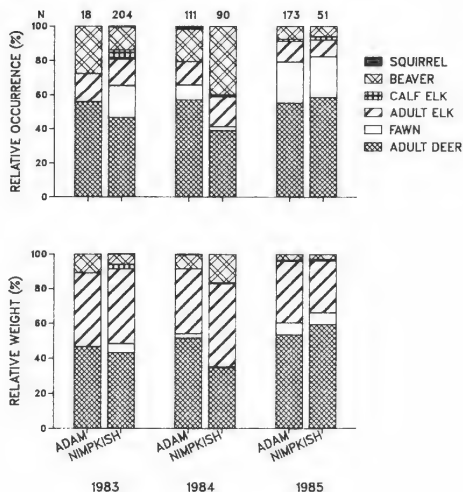


Figure 1. Percent occurrence and relative weight of prey in the diet of wolves from Adam River and Nimpkish River on northern Vancouver Island between 1983 to 1985. Number of scats are indicated above the histograms.

most important prey species in the Nimpkish area, with the exception of 1984, when elk comprised 48 percent of the total prey biomass consumed compared to 35 percent for deer. Relative total weights of beaver and squirrel consumed in the Adam area were small throughout the study period. Similarly, beaver and squirrel in the Nimpkish area comprised small percentages of the total biomass consumed.

To compare diets between seasons, fawns were included with adult deer and calves with adult elk for summer data. Summer and winter diets of wolves for all study years combined were different in both the Adam area ($G = 13.5$, $P \leq 0.01$) and the Nimpkish area ($G = 20.5$, $P \leq 0.01$) (Figure 2). Black-tailed deer was the most frequently detected prey in winter and summer scats from both study areas. Scats from the two

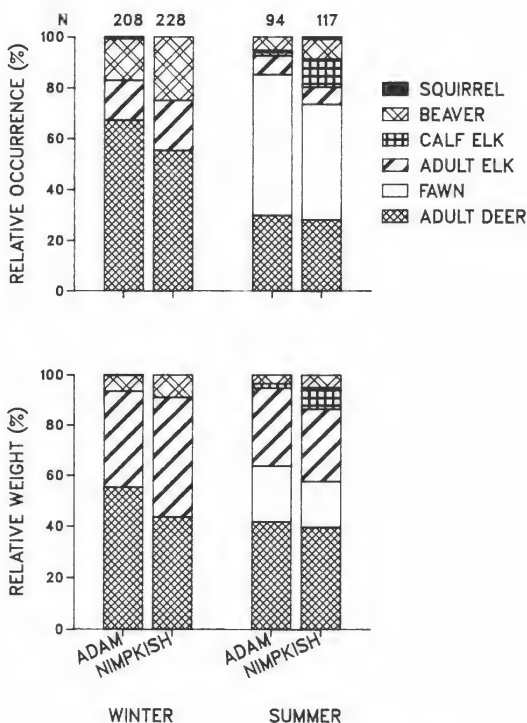


Figure 2. Percent occurrence and relative weight of prey in summer and winter in the diet of wolves from Adam River and Nimpkish River on northern Vancouver Island between 1983 to 1985. Number of scats are indicated above the histograms.

areas had similar frequencies of fawn black-tailed deer which was the most frequently detected food type in summer scats from both the Nimpkish River Valley (45%) and the Adam River Valley (55%). Adult elk hair occurred with similar frequencies in both study areas in winter and summer scats. Beaver hair occurred more frequently in winter scats than in summer scats for both areas. The occurrence of each prey type was similar for the Adam and Nimpkish areas in summer ($G = 9.5$, $P = 0.09$) but in winter adult elk and beaver occurred with greater frequencies in scats from the Nimpkish area than in scats from the Adam area ($G = 10.2$, $P = 0.02$). Black-tailed deer accounted for the greatest percentage of biomass consumed by wolves in winter and summer in the Adam area (Figure 2). In the Nimpkish area, elk comprised the greatest percentage of biomass consumed in winter; however, deer accounted for the greatest percentage of biomass consumed in summer.

Diets of wolves varied among years in both the Adam area ($G = 32.1$, $P \leq 0.01$) and Nimpkish area ($G = 55.1$, $P \leq 0.01$). The occurrence of black-tailed deer in scats from the Adam area increased by 23 percent between 1983 and 1985 and that of beaver hair decreased by 20 percent. In the Nimpkish area, the occurrence of black-tailed deer decreased by 24 percent between 1983 and 1984. During this same period there was a 27 percent increase in the occurrence of beaver. From 1984 to 1985 the occurrence of black-tailed deer increased by 40 percent and beaver decreased by 34 percent.

Discussion

Black-tailed deer are the most important prey of wolves on Vancouver Island. Comparisons of summer and winter diets indicate that wolves on northern Vancouver Island vary their use of prey species and age-classes on a seasonal basis. Deer fawns and elk calves were important prey during summer corroborating other studies in which young ungulates are a substantial proportion of the diets of wolves (Cowan 1947, Theberge *et al.*

1978, Scott and Shackleton 1980, Fritts and Mech 1981, Carbyn 1983).

In contrast to other regions where beaver are prey mainly during summer (Pimlott 1967, Theberge *et al.* 1978), beaver were most frequent in winter scats of wolves on northern Vancouver Island. This winter use of beaver likely occurs because of the mild climate on Vancouver Island which ensures beaver are available all year. Scott and Shackleton's (1980) study in the Adam River Valley during 1978 did not find use of beaver by wolves during summer. However, beaver occurred in summer scats of both Adam and Nimpkish wolves in 1983-1985. Differences between our results and Scott and Shackleton's (1980) may be due to decreases in the density of deer since 1979 (Atkinson and Janz 1986).

Since 1983, deer densities have increased in the Nimpkish Valley (Janz and Hatter 1986). This renewed availability of black-tailed deer is reflected in the scat contents of wolves from the Nimpkish Valley. In 1985, the frequency of occurrence of black-tailed deer in wolf scats increased by 40 percent over the previous year. A similar pattern is apparent in the Adam Valley where the deer population has fluctuated in an increasing direction (Janz and Hatter 1986). The frequency of occurrence of deer in scats from the Adam Valley increased between 1983 and 1985. Wolves on northern Vancouver Island used black-tailed deer as their primary prey between 1983 and 1985. When the relative abundance of deer was low, wolves increased their use of alternate prey types, specifically beaver. Increased use of beaver when white-tailed deer (*Odocoileus virginianus*) densities were low was also reported by Theberge *et al.* (1978).

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Uptake of Tritiated Groundwater by Black Locust Trees

Abstract

Artificially planted trees have survived for four decades in the very dry climate of south-central Washington without irrigation. It is generally believed that long-time tree survival depends on root contact with groundwater but this assumption had not been critically evaluated. Leafwater from trees growing at a location where groundwater was 7.7 m below the surface had elevated levels of tritium. The well water also had elevated levels of tritium indicating that some of the tritium measured in tree leaf water was obtained from root contact with tritiated groundwater. Tritium concentrations in leaf water were greatest in August when sources of tritium other than groundwater are least abundant, indicating that the trees relied most heavily on groundwater during the hottest and driest season of the year.

Introduction

The climate of the U.S. Department of Energy's Hanford Site in south-central Washington is characterized by low (16 cm) annual precipitation and hot, dry summers (Stone *et al.* 1983). The natural vegetation consists mostly of sagebrush, *Artemisia tridentata*, and several species of drought tolerant grasses. However, introduced deciduous trees will grow when planted and irrigated. In the years prior to the acquisition of the land by the federal government, deciduous trees, especially black locust, *Robinia pseudo-acacia*, had been planted and irrigated in the vicinity of farm buildings to provide shade and wind protection. Following land acquisition in 1943, the farms were abandoned, irrigation ceased, and the land was used as a buffer zone around nuclear material production facilities. Over the past four decades many of the trees have died. The survivors were believed to have root access to groundwater which allowed them to meet their water requirements during the hot, dry, summer months. Although it was generally accepted that tree survival depended upon access to groundwater, this had never been adequately demonstrated because there was no way to distinguish the two major sources of tree water, namely that contributed to the upper meter or so of the root zone by annual rainfall from that contributed from deeper soil strata by root contact with groundwater.

One way to distinguish the two possible sources of tree water is to tag groundwater with tritium and then analyze leaf water. Tritium is present in groundwater on the Hanford Site but

it had not been used as an experimental technique (McCormack and Carlile 1984).

Methods

In a preliminary survey conducted during the summer of 1985, leaf water was collected from trees at widely scattered locations across the Hanford Site. The survey indicated that a few black locust trees, growing near the 100 K area, had the greatest concentrations of tritium (Figure 1). However, the depth to groundwater beneath the trees was not known. In April 1986, a well, 16 m deep, was bored near these trees and designated as well K-31.

In May, six black locust trees spaced 10 meters or more apart, but all located within a 50-m radius of well K-31, were selected for leaf water sampling. Leaf water was obtained from small branches clipped from each tree monthly from June through September. Leafy twigs were cut from the freshly severed branches and placed inside translucent plastic bags. Each bag was tightly sealed and then placed in direct sunlight for four to five hours. Water droplets that accumulated on the inside surface of the bags were drained into a bottle. The accumulated water was purified by distillation in the laboratory and the distillate analyzed for tritium (Rickard and Kirby 1987). A sample of groundwater was collected from well K-31 on the same day the leaves were taken from the trees. The groundwater was distilled and analyzed in the same way as leaf water.

One tree from a group of non-irrigated black locust trees located outside the boundaries of the Hanford Site at Horn Rapids Park, near the Yakima River, was used as a control or background

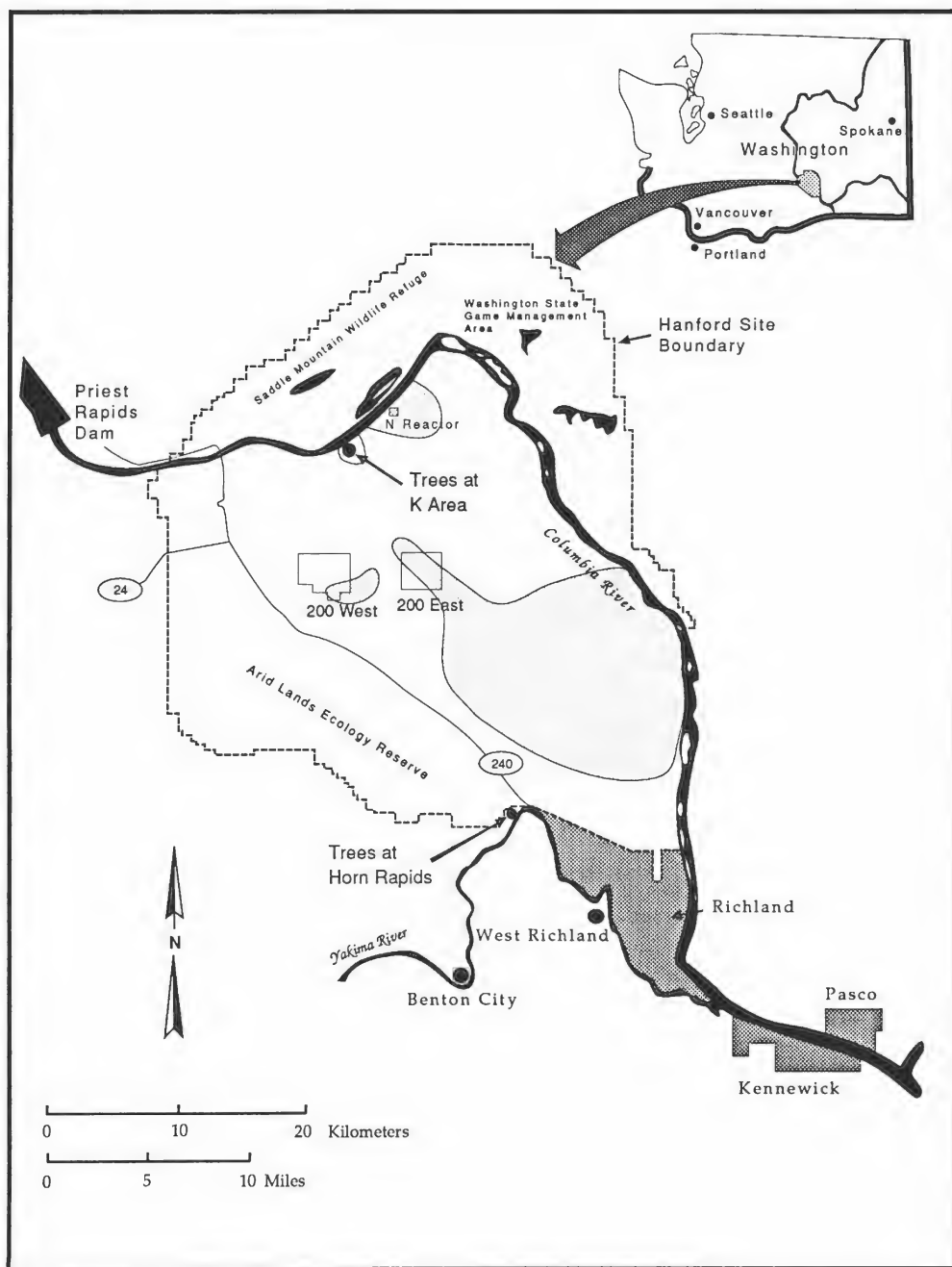


Figure 1. Map of the Hanford Site and Adjacent Areas Showing the Location of Black Locust Trees Sampled for Tritium and the Approximate Extent of Tritiated Groundwater (lightly stippled).

sample (Figure 1). Tritium concentrations are reported as picocuries (10^{-12} curies) per liter of water.

Results and Discussion

The water level in well K-31 stood at 7.7 m below the ground surface. The tritium concentration of the well water was relatively stable throughout the summer and averaged 4500 pCi per liter (Table 1). All the trees sampled near well K-31 had leaf water concentrations of tritium greater than 3000 pCi per liter, and as high as 12,000, indicating root contact with tritiated groundwater (Table 1). In contrast, the tree at Horn Rapids Park, beyond the boundaries of groundwater contamination, had background tritium concentrations ranging between 200 and 800 pCi per liter of leaf water.

It was thought that tritium concentrations in leaf water would be less than those measured in groundwater at all times because the trees also have root access to water introduced to the ground in rainfall, which characteristically contains low levels of tritium. Therefore, the tritiated groundwater, when it appeared in leaf water,

would be expected to be somewhat diluted by rain water input. However, at times tritium concentrations in leaf water were greater than those in groundwater (Table 1). This suggested to us that the root systems of the trees had access to zones of groundwater with higher tritium concentrations than those measured in the well water.

On the average, the highest concentrations of tritium were measured in the leaf water samples collected in August when water sources other than groundwater were least plentiful, indicating that trees relied most heavily on groundwater late in the summer (Table 1). Similar findings were obtained during a similar survey conducted in a natural oak-hickory forest in eastern Kentucky (Kalisz *et al.* 1988).

A conclusion is that black locust trees rely on groundwater throughout the leaf-bearing season but most heavily in late summer.

Acknowledgments

This work was supported by the U.S. Department of Energy under Contract DE-AC06-76RLO 1830. R. E. Fitzner collected the tree leaves and his contributions are gratefully acknowledged.

TABLE 1. Tritium concentrations (pCi/L of leaf water) extracted from six black locust trees growing near well K-31 on the Hanford Site in the summer of 1986. Values are rounded to 2 significant figures. Counting errors ($\pm 1\sigma$) were within 10% of the reported values.

	Tree Identification Numbers						Mean	groundwater
	tree 1	tree 2	tree 3	tree 4	tree 5	tree 6		
June	4600	5500	7000	5900	6600	7600	6200	4500
July	3300	5800	10000	5300	3600	9500	6200	4400
August	5200	7400	12000	4700	5300	10000	7400	4400
September	3000	5400	4500	3600	4000	6400	4500	4600
Mean	4000	6000	8400	4900	4900	8400	6100	4500

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Aspects of Forster's Tern (*Sterna forsteri*) Reproduction on Cobblestone Islands in Southcentral Washington

Abstract

Reproductive variables of the Forster's tern (*Sterna forsteri*), a species normally found nesting in marshes, were studied during the 1985 breeding season on cobblestone islands on the Hanford Reach of the Columbia River in southcentral Washington. In a colony of 81 active nests, average clutch size was $2.9 (\pm 0.39; 1 \text{ S.D.})$. Nesting success, based on successful chick hatchings (at least 1 chick per nest), was 71.6 percent and exceeded that reported for marsh studies.

Introduction

The Forster's tern (*Sterna forsteri*) has been described in relation to its breeding behavior as a bird that nests principally in marshes, and only on occasion on gravelly or sandy beaches or bars (Bent 1921, McNicholl 1971). On the Hanford Reach of the Columbia River in southcentral Washington, Forster's terns nest on cobblestone islands. This situation provides an opportunity to compare data on reproductive success obtained from a dry-land colony to that obtained from marsh-nesting colonies.

Study Area

Hanford Reach Islands Nos. 18, 19, and 20 have a history of nesting site use by Forster's terns (Thompson and Tabor 1981) (Figure 1). Because these islands are in the McNary National Wildlife Refuge, public access is restricted to them from 1 February to 30 June. During the 1985 nesting season, two Forster's tern colonies, 18A and 18B, were located on Island No. 18 and one on Island No. 19. These islands consist mostly of cobble substrate (Fickeisen *et al.* 1980) and at low river levels are approximately 37.2 and 50.9 ha in size, respectively (Dewaard 1981). Island No. 18 often is split into two islands during the spring when upstream Priest Rapids Dam maintains high river flows. The colonies were located on the upstream ends of the islands, just above the high water mark resulting from dam operation. Colony 18B was located on the upstream end of the split-off portion of Island No. 18 and was adjacent to a mixed colony of ring-billed gulls (*Larus delawarensis*) and California gulls (*L.*

californicus). When river levels lowered, gulls also flocked at the extreme upstream tip of the islands.

Several plant communities exist on each of the islands (Hanson and Eberhardt 1971, Fickeisen *et al.* 1980, Dewaard 1981). At all three colony locations terns nested mainly in areas of scattered vegetation dominated by absinthie (*Artemisia absinthium*), northern buckwheat (*Eriogonum compositum*), and Columbia River grindelia (*Grindelia columbiana*). Small amounts of lupine (*Lupinus* sp.) and mulberry (*Morus alba*) were also present. Later in the breeding season, as river levels lowered and chicks left the colony nesting area, willow (*Salix exigua*), that earlier in the season were generally inundated, became important as cover.

Methods and Materials

During May through July 1985, colony 18A was visited on an almost daily basis. Data were obtained both from ground surveys and approximately 145 hours of observations from an elevated blind. Because visits to the other two colonies were less frequent, they were excluded from data analysis. The active nest count at colony 18A represented nests containing at least one egg. A scaled map showing nest locations was made to aid identification and assess colony structure for comparison with marsh colonies (Figure 2). The map includes some nests of incomplete construction that were abandoned prior to egg laying. Internest distances were measured from the nearest edge of each nest. Nest spatial relationships were assessed using the method of Clark and Evans (1954).

Average clutch size per nest was determined using nests only with completed clutches. Nests

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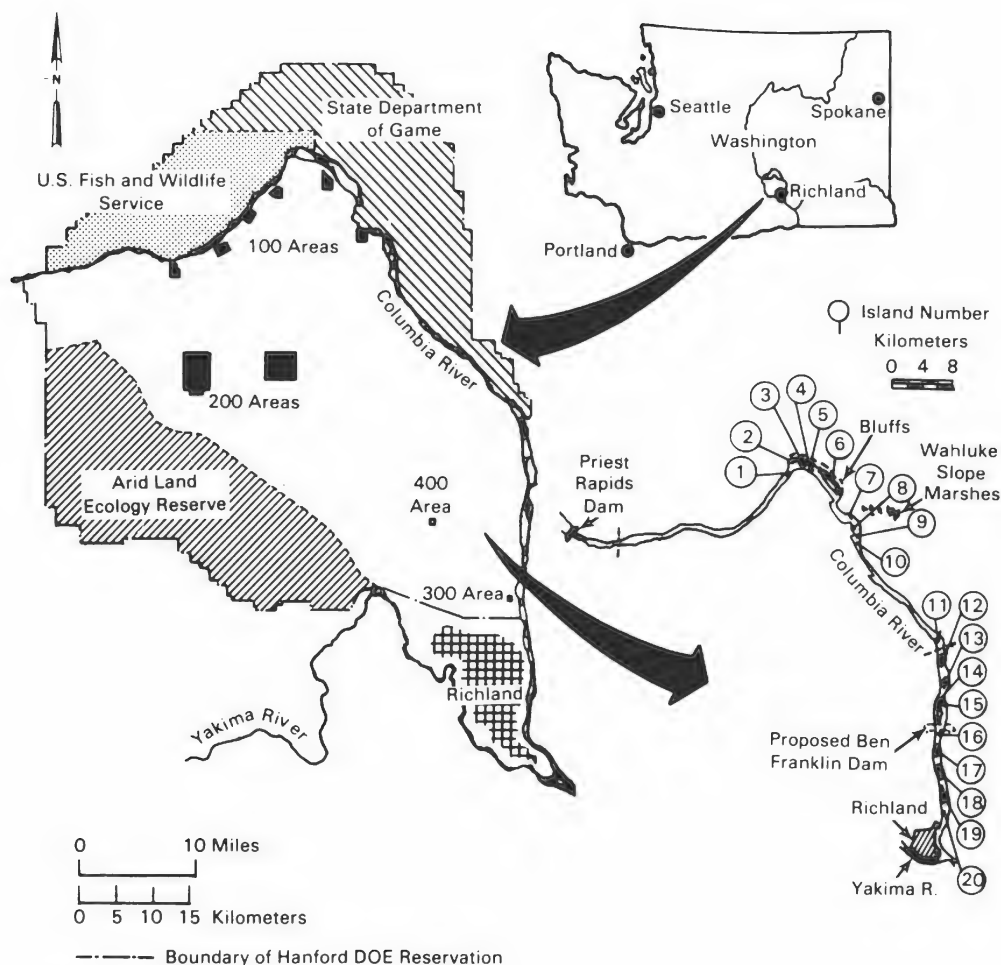


Figure 1. Hanford Reach of the Columbia River.

considered to have incomplete clutches appeared partially constructed and were unoccupied. Hatching success of each egg and the fate of each chick prior to its leaving the colony were recorded. Productivity was calculated as the proportion of chicks that were reared successfully up to the time of leaving the colony nesting areas per number of eggs laid in the colony. Comparisons between the productivity data of this study and those of a marsh study (McNicholl 1971) were made using the goodness of fit G-test of Sokal and Rohlf (1981).

Results

Colony 18A consisted of 81 active nests. More than half of the nests were constructed directly atop only the cobble substrate. Others were constructed in association with some of the scattered vegetation, principally northern buckwheat. Nest density varied with location in the colony and ranged from approximately 0.01-0.05 nests per m^2 ; nest density appeared to be associated with vegetation density (Figure 2). The mean interest (nearest neighbor) distance was 3.5 ± 1.9 m (1 S.D.), with a range of 0.9-12.7 m. The minimum

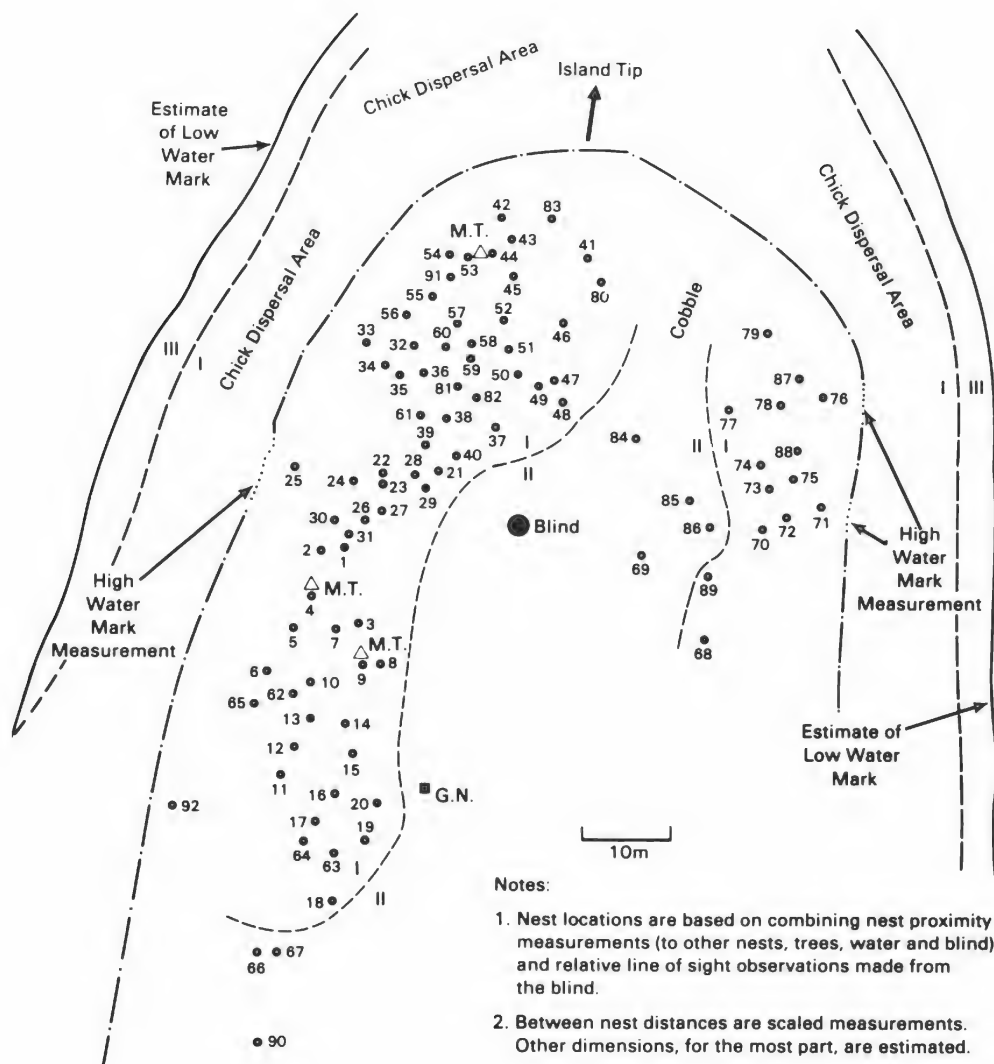


Figure 2. Relative nest locations at colony 18A. Legend: I = absinthe community; II = northern buckwheat community; III = willow community; G.N. = ring-billed gull nest; and M.T. = mulberry tree.

distance measured (0.9 m) involved an unoccupied nest; whereas, the minimum distance between two adjacent occupied nests was 1.8 m.

Mean clutch size and various indices of reproductive success are presented in Table 1. At colony 18A, the most frequent clutch size was three (61 nests). The mean incubation time was 24 days (based on 4 nests and 6 eggs; range 23-

26 d). The incubation period for the colony extended for roughly eight weeks with most chicks (86%) hatching within a two week interval. Young stayed in the nest vicinity for an average of four days. Thereafter, they were led by adults to areas outside the colony proper (Figure 2) where they were cared for until fledging (Hall 1988). From observations of newly fledged chicks, fledging

TABLE 1. Productivity data of Forster's terns nesting on a cobblestone island and in a marsh.

Variable	Present Study		McNicholl (1971)	
	Number	Percent	Number	Percent
Colony Size (nests)	81		85	
Eggs Laid	220	100.0	217	100.0
Clutch Size (S.D./N)	2.9 ($\pm 0.39/74$)		2.7 ($\pm 0.47/77$)	
Eggs Hatched	154	70.0	33	15.2
Eggs Not Hatched (cause independent of predation)	66	30.0	168	77.4
Eggs Lost to Predation	0	0.0	16	7.3
Chick Mortality Prior to Leaving the Colony	25	16.2	18	54.5
Chick Productivity Prior to Leaving the Colony	129	58.6	15	6.9
Successful Nests*	58	71.6	14	16.5

*Nests that hatched at least 1 chick, whether or not the chick survived to fledge.

was estimated to take place four to five weeks after hatching. Productivity based on the number of chicks fledging was not obtained, as fledging occurred away from the immediate nesting area.

Discussion

In the marsh, Forster's terns build their nests predominantly atop muskrat (*Ondatra zibethica*) houses, active and inactive, and floating vegetation, with frequently more than one nest located on a substrate (Bergman *et al.* 1970, McNicholl 1971). Both Bergman *et al.* and McNicholl found evidence of social nesting where nest-site selection appeared dependent on social attraction and not just nest-site availability. McNicholl determined mean internest (center to center) distances of 0.8 m and 6.8 m, for nests on muskrat houses and floating rafts of mostly dead vegetation, respectively; but more significant was his finding that nests floating independently were still only a mean distance of 6.7 m away from nests on muskrat houses and rafts. The terns that nested independently, nested in closer association to the nests on the muskrat houses and rafts than would be expected based on the amount of available nesting sites (McNicholl 1971). At colony 18A, the density of nests varied and was perhaps somewhat related to the density of the vegetation and the cover it provided. Mean internest

distances were approximately halfway between those reported by McNicholl.

The spatial relationship of nests within a Forster's tern colony appears to be constrained by both physical and social features of the environment. Social attraction causes the terns to aggregate together as a colony; whereas, the availability of suitable nest sites and the existence of maximum and minimum acceptable distances to a neighbor determines whether the tern nests will exhibit an aggregated, random, or uniformly spaced distribution (Clark and Evans 1954). In colony 18A where low nest density occurred (0.01 nests per m²), nests tended to be aggregated; whereas, at high nest density (0.05 nests per m²), the tendency was for nests to be uniformly spaced. Thus, social attraction appears to be important, but in high nest density situations the terns attempt to achieve maximum spacing.

McNicholl (1971) obtained similar results for colony size, total eggs laid, and average clutch size for Forster's terns nesting in a marsh (Table 1); although, in his colony the terns bred asynchronously so that the colony size at any one time was smaller than that listed in Table 1. McNicholl's average clutch size is based on data from two nesting seasons and also reflects eliminating nests that had incomplete clutches (generally only 1 egg present). Clutch size distributions between this study and McNicholl's were not different ($G = 2.415$, $df = 2$, $P > 0.1$).

McNicholl believed clutch sizes of greater than three reflected the work of more than one female. My only nest with four eggs supported this observation. Two eggs were laid at least five days later than the first two eggs. The mean incubation time obtained in the present study (24 days) is the same interval obtained by Bergman *et al.* (1970) and McNicholl (1983). Thus, terns do not appear to make any adjustments in clutch size or incubation time dependent on nesting in different habitats.

There was a difference in the proportion of eggs hatched between the two studies ($G = 142.404$, $df = 1$, $P < 0.001$). In the present study, egg predation was not observed until colony size was reduced to six active nests and only included those eggs of nests already unoccupied. Prior to this, the adult terns effectively mobbed potential aerial predators, principally gulls. Additionally, the swift current and depth of the Columbia could act as a barrier to the movement by ground predators onto the islands. Causes for abandoning nests still containing eggs were not determined, but could have involved desertion caused by disturbance or mortality of one or both of the incubating adults. In the marsh, predation (mostly mink, *Mustela vison*) accounts for some of the egg loss; however, the bulk of the loss (138 eggs) is a direct result of wave action (McNicholl 1971).

I could not assign any chick mortality directly to predation (Table 1). Chicks found dead in the colony were generally only a day or so old, still present in the nest cup, and without signs of physical abuse. The most probable cause of death was hyperthermia due to exposure during disturbances. During a period of cold, wet weather, disturbance pressure caused by gulls and my own presence possibly led to nest inattentiveness by the adults at a time when the young chicks had not developed an adequate ability to thermoregulate. As with egg loss, chick mortality in the marsh is also proportionately high when compared to the present study ($G = 19.119$, $df = 1$, $P < 0.001$). In the marsh, 10 of the 18 chicks found dead were killed by predators and six died during a storm (McNicholl 1971).

Overall, productivity was greater in the present study than in the marsh. Of the 220 eggs laid in colony 18A, 58.6 percent (129) survived as chicks to leave the nesting area compared to 6.9 percent in McNicholl's (1971) marsh study.

In the marsh study of Bergman *et al.* (1970), nesting success was only 12 percent (13 of 107 nests). In this latter study, nesting success was based on the hatching of at least one chick at a nest site whose continued presence was noted during subsequent weekly surveys. The causes of nesting failure were similar to those reported by McNicholl. A similar measure of nesting success, calculated for the present study, was 71.6 percent; whereas, McNicholl reported only 16.5 percent.

Water appears to play a key role in nest site selection and the subsequent reproductive success of the Forster's tern. For large marshes, McNicholl (1971) indicated nests tended to be constructed facing open water; whereas, the terns avoided small marshes (see also Bergman *et al.* 1970). The open water situation allows exposure to the action of wind and waves. McNicholl identified weather as the most important factor determining tern nesting success. Because of the proximity of the tern nests to water in a marsh, they are quite susceptible to wave damage (McNicholl 1971). On the Hanford Reach, the dam-regulated, early spring high river levels can be a larger problem than weather. Depending on how long high river levels are maintained, initial nesting attempts could be hindered and the chances of successful re-nesting diminished by reducing the amount of available nesting habitat and destroying early nests and eggs. For the 1985 nesting season, however, water levels did not appear to interfere with nesting. Thus, although they were nesting in what is considered for them an atypical habitat, Forster's terns on the Hanford Reach islands had a greater nesting success than reported for this species in marsh habitat.

Acknowledgments

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A Probable Sixth Leavenworth Glacial Substage in the Icicle-Chiwaukum Creeks Area, North Cascade Range, Washington

Abstract

In the valleys of the Icicle-Chiwaukum creeks area on the eastern slope of the North Cascade Range, moraines with pronounced constructional topography are representative of the last glaciation, the Leavenworth glaciation. Recession from the Leavenworth maximum was followed by several lesser stillstands or readvances. The Larch Lake moraine at the head of Chiwaukum Creek reaches 1737 m altitude and lies between the Leavenworth V moraine and moraines of Neoglacial age. On and behind the Larch Lake moraine the ca. 11,250-year-old Glacier Peak tephra is found beneath the 6900-year-old Mazama ash. Moraines with preservation, form, and relative position nearly identical to that of the Larch Lake moraine occur in the Icicle Creek drainage beyond the fallout limit of the Glacier Peak tephra. Because the Larch Lake moraine was built prior to late-glacial eruptions of Glacier Peak but after the Leavenworth V substage, it apparently represents a previously unrecognized substage termed Leavenworth VI.

Introduction

Icicle and Chiwaukum Creeks are in the southern Wenatchee River drainage, Chelan County (Figure 1). Along Icicle Creek multiple-end moraines with pronounced constructional topography and associated outwash bodies permit subdivision of the latest glaciation (Leavenworth) into four substages (Long and Porter 1968, Porter 1969). Waitt (1977) found a fourth Leavenworth-age moraine a mile behind the Leavenworth III in lower Icicle Creek valley. Recession from the Leavenworth maximum was followed by several lesser readvances. Glaciers during the Leavenworth I, II, III, and IV substages were long valley glaciers (longest glacier 48 km). During the Leavenworth V substage they were short valley glaciers (longest glacier 12 km in Eightmile Creek).

As described by Porter (1969), the type Leavenworth V deposit is an arcuate moraine complex built by the Rat Creek glacier at the junction of Icicle Creek and Rat Creek. The inner of two moraines forms a continuous loop, crossed by Rat Creek at its lowest point at 549 m altitude, and is the lowest Leavenworth V moraine in Icicle Creek drainage. Distribution of Leavenworth V moraines in Icicle Creek is shown on the location map of Icicle and Chiwaukum Creek drainages (Figure 1).

While mapping Leavenworth V deposits along Icicle Creek, I recognized moraines behind the Leavenworth V moraines but below those in the highest cirques. The highest moraines are very fresh, as are the bedrock surfaces within

their confines, suggesting that they are Neoglacial in age. The Leavenworth V and intermediate moraines have a thin soil which supports old-growth conifers, but the Neoglacial moraines have only incipient soil profiles and sparse vegetation. The intermediate moraines could represent either a previously unrecognized sixth Leavenworth substage or a post-Leavenworth advance. A reasonable solution to the problem was found in 1987 in neighboring Chiwaukum Creek valley.

Observations

The maximum length of the Icicle Creek glacier of Leavenworth V age, as measured from Josephine Lake at the source of Icicle Creek, was 10.5 km, compared to 48 km for the Leavenworth I. A moraine thought to be the terminal moraine of the Leavenworth V glacier in Icicle Creek lies at the junction of Icicle Creek and Doughgod Creek at 945 m altitude (Figure 1).

Page (1939) described a moraine-like mass just below the mouth of Glacier Creek that consists of angular schist blocks piled up in transverse fashion across the valley. This mass was thought by Page to be a recessional moraine, or one marking the termination of the glacier occupying upper Chiwaukum Canyon. Leavenworth V ice along upper Chiwaukum Creek apparently terminated here at 1158 m, about 1 km below the mouth of Glacier Creek.

The moraine forms a continuous loop which is incised by Chiwaukum Creek to a depth of about 8 m (visible on USDA serial photographs

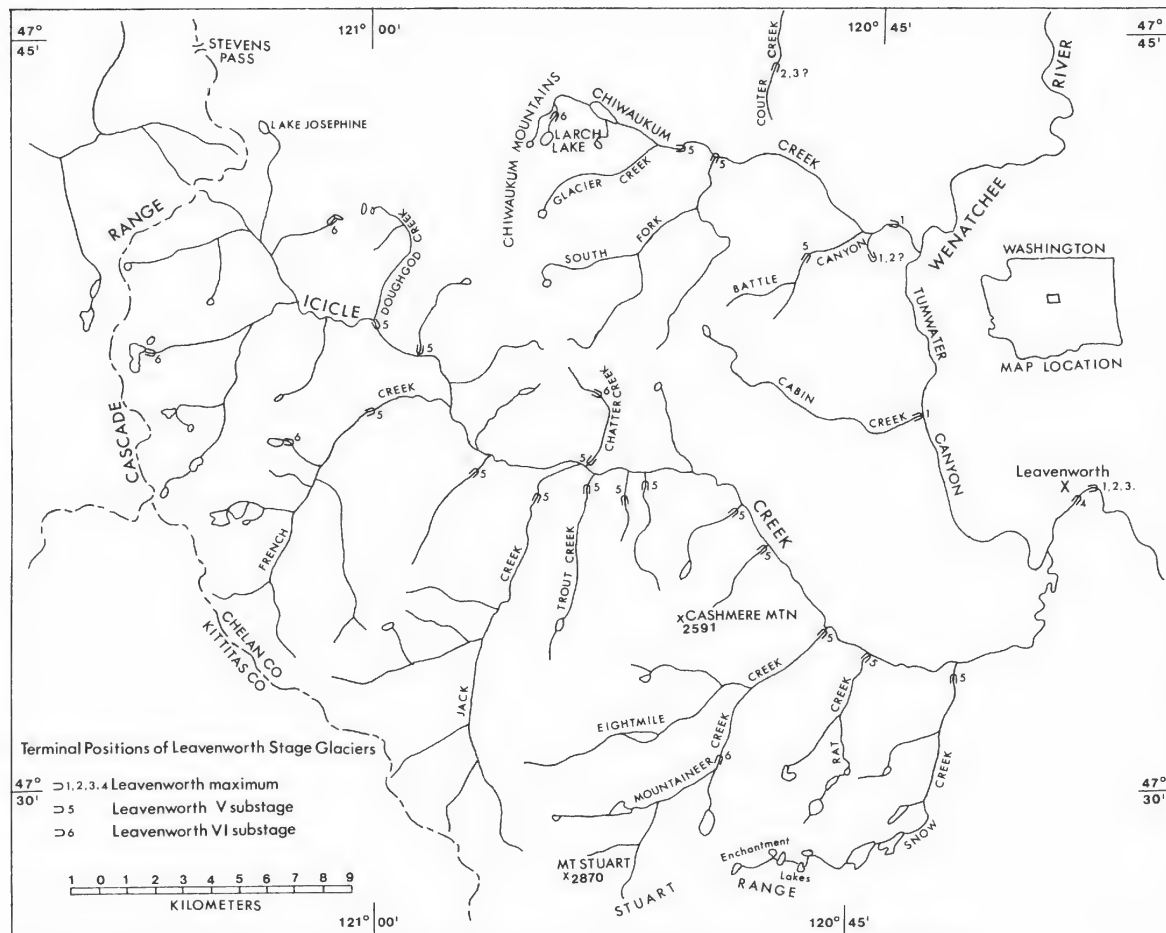


Figure 1. Location of Icicle and Chiwaukum Creek drainages and terminal position of glaciers.

1986 flight). A large swampy area behind the moraine may have been a lake. A well-defined segment of moraine remains against the south valley wall and rises 45 m above the swamp. Evidently the central part of the moraine has been eroded, thereby exposing its broad base, which rises as much as 10 m above the swamp and consists of fresh rubble and angular blocks up to 8 m in diameter.

A sharp-crested, well-developed lateral moraine (altitude 1675 m) lies 90 m above the west end of Chiwaukum Lake. This moraine, recognized by Merrill (1966), is here interpreted as the right-lateral moraine of the Leavenworth V glacier. From its (1830 m) altitude, north aspect, and large size of the Jason Lakes cirque, it is clear that ice from Jason Lakes joined the Chiwaukum Creek glacier over Honour Lake at a point only 2 km above the mouth of Glacier Creek (Figure 2). The Glacier Creek glacier joined the Chiwaukum Creek glacier farther downvalley and was the most important tributary.

Larch Lake Moraine

Larch Lake is a tarn at an altitude of 1852 m (6048 ft) behind a multiple terminal moraine in the Chiwaukum Creek valley-head cirque (Figure 2). The Larch Lake moraine reaches an altitude of 1737 m and lies 8 km upvalley from the Leavenworth V moraine. At Larch Lake a yellowish-brown pumiceous tephra layer underlies a thick pale-brown fine ash in a surface locality just behind the innermost moraine. A stratigraphic section was obtained in a wet meadow inside the Larch Lake moraine at the tephra sample site (Figure 2).

As shown in Figure 3, the base of the section is in dark gray, layered lacustrine silt, the deposit of a small lake formerly dammed by the moraine. The silt is overlain by 30 cm of tephra consisting of yellowish-brown and strong brown (when wet) pumice lapilli up to 8 mm in diameter. The tephra is covered by 43 cm of dark gray sand and gravel and 30 cm of black sandy organic sediment. Above is 70 cm of strong orange to yellowish-brown (when wet) fine ash capped by about 30 cm of fine loamy sand with many roots. The unusual thickness of the volcanic ash layers is most likely due to fluvial reworking and concentration of the ashes.

Cup Lake Moraine

As described by Merrill (1966, p. 8), a moraine damming Cup Lake at an altitude of 1964 m (6443 ft), which he provisionally assigned a Neoglacial age, lies in the highest cirque of the Chiwaukum Creek drainage (Figure 4). The Larch Lake moraine separates the Larch Lake cirque from the stream draining Cup Lake. The Cup Lake moraine is very bouldery, exceedingly fresh, and shows little or no soil development. Lichen cover on moraine boulders is discontinuous and other vegetation is absent. The Cup Lake cirque has only small talus cones, in contrast to much larger talus cones just downstream on the east-facing valley wall. Because the Mazama ash apparently is absent on or behind the moraine but is present on the steep slope immediately beyond it, and because there is no hint of a stream notch, the Cup Lake moraine is considered to be late Neoglacial (late Little Ice Age) in age.

Discussion

The tephra layers were identified in the field as Glacier Peak lapilli pumice and Mazama silty ash on the basis of grain size, color, distribution and stratigraphic position. Three principal layers of pumiceous tephra, resulting from multiple eruptions of the Glacier Peak volcano in late-glacial time, cover much of the landscape in the eastern North Cascade Range (Porter 1978). In this area the Glacier Peak tephra, as shown by Porter (1978), consists largely of lapilli pumice; the grain size decreases away from the volcano, with fine ash being predominant only along the distal margins of the deposit and east of the Columbia River. Available ^{14}C dates indicate that the Glacier Peak tephra were deposited about 11,250 year B.P. (Porter *et al.* 1983). The lapilli pumice at Larch Lake could only have come from Glacier Peak, because lapilli pumice layers from any other source have not been recognized in this part of the North Cascades.

At the Larch Lake locality, the 6900-year-old Mazama tephra is a fine volcanic ash, light-yellowish-brown or tan in color when dry, and apparently reworked and concentrated to a thickness of 70 cm. The only volcanic ash megascopically similar to the Mazama that could be mistaken for it is the 3400-year-old Mount St. Helens Yn ash, which generally is found only as a thin silt layer above the Mazama in this part of

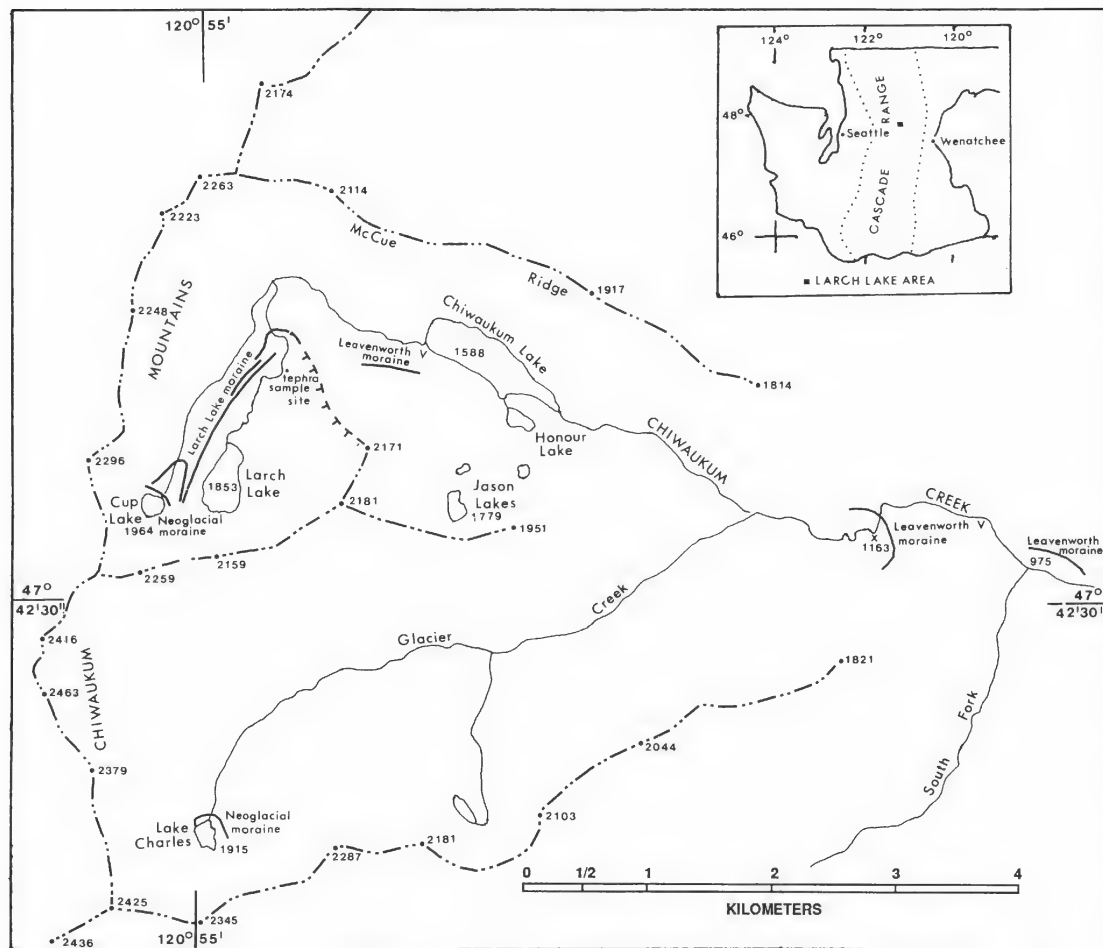


Figure 2. Map showing position of moraines at Larch Lake and vicinity.

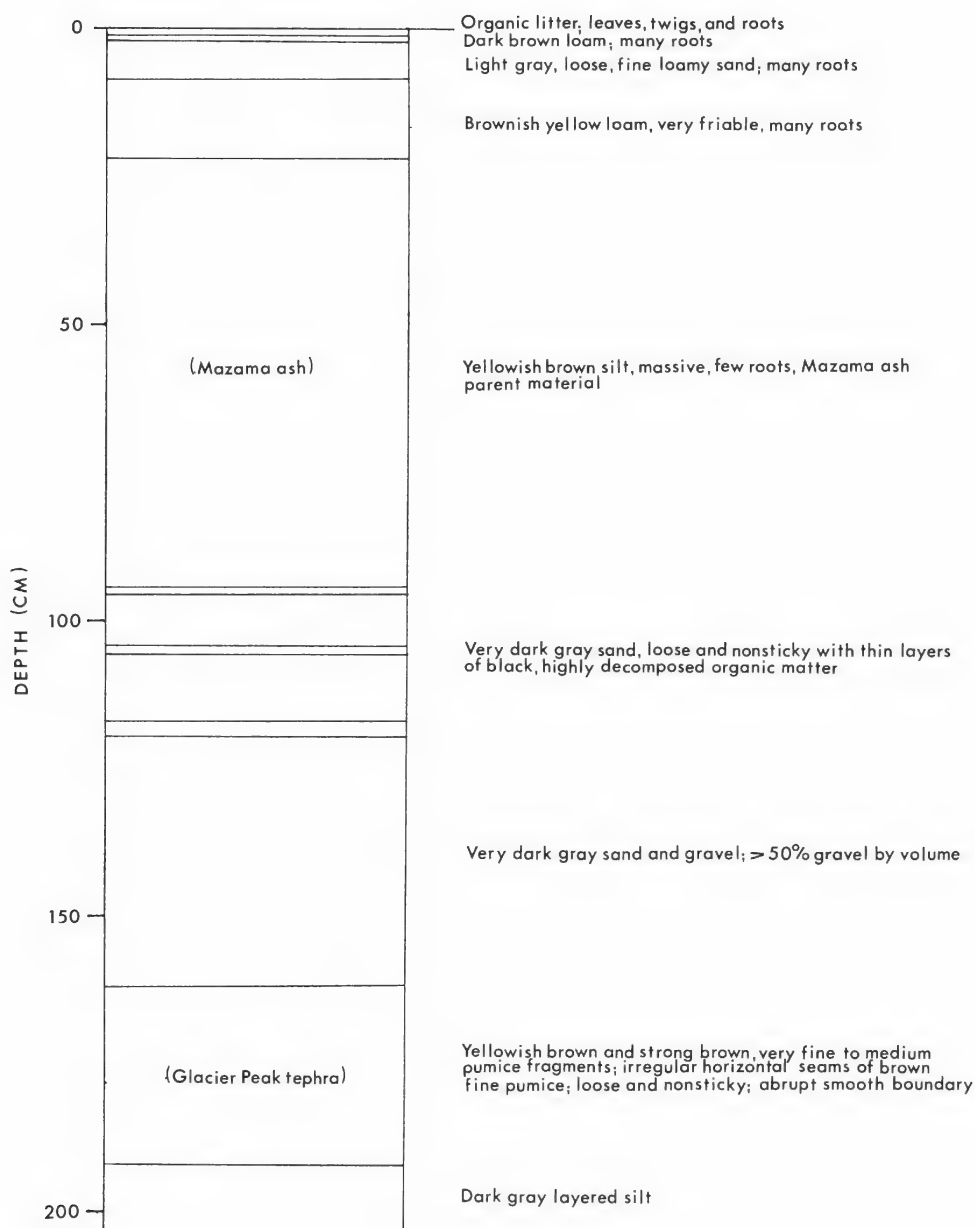


Figure 3. Stratigraphic succession at a wet meadow inside Larch Lake moraine at head of Chiwaukum Creek (See Figure 2 for location).



Figure 4. Looking south to the head of Chiwaukum Creek, with Cup Lake cirque at view center and Larch Lake in cirque at middle left foreground. Tree-covered crest of Larch Lake moraine extends diagonally downward and separates the Larch Lake cirque from the stream draining Cup Lake.

the Cascades. Because the lowermost tephra layer at a depth of 170 cm is an airfall lapilli pumice easily identifiable as from Glacier Peak, the Larch Lake moraine must be older than about 11,250 years B.P.

Waite *et al.* (1982) described two moraine sets in the upper Enchantment Lakes Basin of the Stuart Range, which drains into Snow Creek tributary to lower Icicle Creek (Figure 1). Each moraine records an episode of glacier advance after the end of the Leavenworth glaciation. The outer moraine set, the Brisingamen, lies at 2310 m, about 8 km behind and 1760 m above the type Leavenworth V moraine at the mouth of Rat Creek. Apparently there are no moraines between the Brisingamen moraine and the Rat Creek moraine. The inner moraine set, the Brynhild, lies immediately beyond Snow Creek Glacier. It is only slightly weathered, lacks a soil, and is almost devoid of lichens. The Brynhild moraines evidently postdate Mount St. Helens tephra Wn (500 years old; 1480 AD), which lies only beyond the inner moraine set, and therefore are Neoglacial in age. The Brisingamen moraine is weathered, and on and behind it the 6900-years-old Mazama ash is present beneath the Mount St. Helens Yn (3400 years old) and Wn tephra layers. Tephra from Glacier Peak eruptions was not found in the Enchantment Lakes Basin, which apparently lies south of the recognized limits of Glacier Peak tephra. Waitt *et al.* (1982) noted that despite more than seven millennia of weathering, the rock surface behind the Brisingamen moraine is measurably less weathered than the surface beyond, which was last glaciated during the Leavenworth V (Rat Creek) advance about 13,000 years ago. These data led them to assign a probable age of early Holocene to the Brisingamen moraine.

As the Larch Lake moraine lies between the Chiwaukum Creek moraine of probable Leaven-

worth V age and the Cup Lake moraine of Neoglacial age, it occupies a relative position similar to that of the Brisingamen moraine. The Brisingamen moraine predates the 6900-year-old Mazama ashfall, whereas the Larch Lake moraine predates the ca. 11,250-year-old Glacier Peak tephra. Thus, while the Larch Lake moraine can be assigned to latest Leavenworth time, the Brisingamen moraine could represent either an early Holocene glacier advance, as suggested by Waitt *et al.* (1982) or, if correlative with the Larch Lake moraine, it could represent a late Leavenworth event.

Conclusions

Whether the Larch Lake moraine represents a stillstand or readvance of Leavenworth ice is not clear, but the moraine's nearly complete closure and position on the northwest-facing threshold of a large valley-head cirque delimits the ice that built it. Because the Larch Lake moraine lies behind the Leavenworth V moraine in Chiwaukum Creek and has Glacier Peak tephra on and behind it, the moraine was built some time before late-glacial eruptions of Glacier Peak volcano about 11,250 years ago, but after the Leavenworth V substage. The Larch Lake moraine therefore probably represents a previously undescribed sixth Leavenworth substage.

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Use of Domestic Sheep Carrion by Bald Eagles Wintering in the Willamette Valley, Oregon

Abstract

Bald eagles (*Haliaeetus leucocephalus*) wintering in the Willamette Valley, Oregon, are known to feed on live domestic sheep, and have been shot or poisoned while feeding in sheep pastures. Our purpose was to help resolve some of the land-use conflicts surrounding wintering eagles in this area by documenting eagle use of domestic sheep. We conducted weekly (December 1986 through March 1987) counts of foraging eagles at primary foraging locations, made observations of eagle-sheep interactions, and examined eagle castings found at night roosts. Bald eagles fed almost exclusively on sheep carrion and afterbirth that were available throughout the study area but were never observed feeding on live sheep. Eagle numbers peaked at 20 birds with subadults outnumbering adults (68.2% vs. 31.8%) and this peak coincided with the lambing period. Primary feeding locations were pastures bordered by tall (>20 m) cottonwoods (*Populus trichocarpa*) and most were within 7 km of night roosts. Adult eagles were observed feeding in pastures at greater distances from roads than subadults. Landowners should be encouraged to place sheep carcasses in remote areas away from nearby roads to allow feeding by eagles of all ages and divert eagle use from areas where they may be killed. This would also provide winter food in an area that once supported a much larger and diverse prey base for this threatened species.

Introduction

The diet of wintering bald eagles is highly varied and influenced by local and seasonal abundance of prey and weather (McClelland *et al.* 1982, Isaacs and Anthony 1987, Keister *et al.* 1987). Bald eagles are known to feed on cow and deer carrion (Isaacs and Anthony 1987, Isaacs pers. comm.), fish, waterfowl, and small mammals (Hancock 1964, Swisher 1964, Servheen 1975, Stalmaster 1976, Steenhof 1976, Frenzel 1984), domestic chickens and hogs (Southern 1964). Reports of bald eagles feeding on domestic sheep carrion have been limited to the Gulf Islands of British Columbia (Hancock 1964). Agricultural areas where domestic sheep ranching is an important subsistence of local economies offer opportunities to study the importance of sheep carrion as a food base for wintering bald eagles.

In the Willamette Valley, bald eagles have been observed killing live sheep and feeding on sheep carrion (private landowners pers. comm.). Concerns have been expressed over economic

losses associated with eagle depredation on sheep and for the birds' safety; at least six bald eagles have been shot or poisoned during the winters of 1986 and 1987 (G. Anderson, State Game Officer pers. comm.). This study was initiated by the Bureau of Land Management to document bald eagle use of domestic sheep and to help resolve some of the land-use conflicts associated with wintering eagles in this area.

Study Area

Historical Description

Bald eagles were considered common in the Willamette Valley in 1857 (Gabrielson and Jewett 1940). This is consistent with historical descriptions of habitat conditions and food supplies that existed at the time of white settlement. During that period the valley consisted of a mosaic of grasslands, oak savannahs maintained by fire, and conifer forests with natural lakes, ponds and wetlands (Towle 1979, Boyd 1985). This combination of high habitat diversity and mild wet winters once provided eagles with overwintering waterfowl and carrion from abundant populations of white-tailed deer (*Odocoileus virginianus*) and Roosevelt elk (*Cervus elaphus*) (Boyd 1985).

¹Present address: EnviroSphere Company, 10900 NE 8th St., Bellevue, Washington 98004.

Population densities of these species greatly exceeded present conditions (Boyd 1985).

Present Conditions

The Willamette Valley is now a mosaic of pastures grazed by domestic sheep and bordered

by cottonwood, Oregon white oak (*Quercus garryana*), incense cedar (*Libocedrus decurrens*) and low-growing shrubs along fence rows. Bald eagles have been observed feeding in the valley and roosting in the Coburg Hills (Figure 1). A small population of bald eagles has been wintering near Brownsville, Oregon, for the past 20

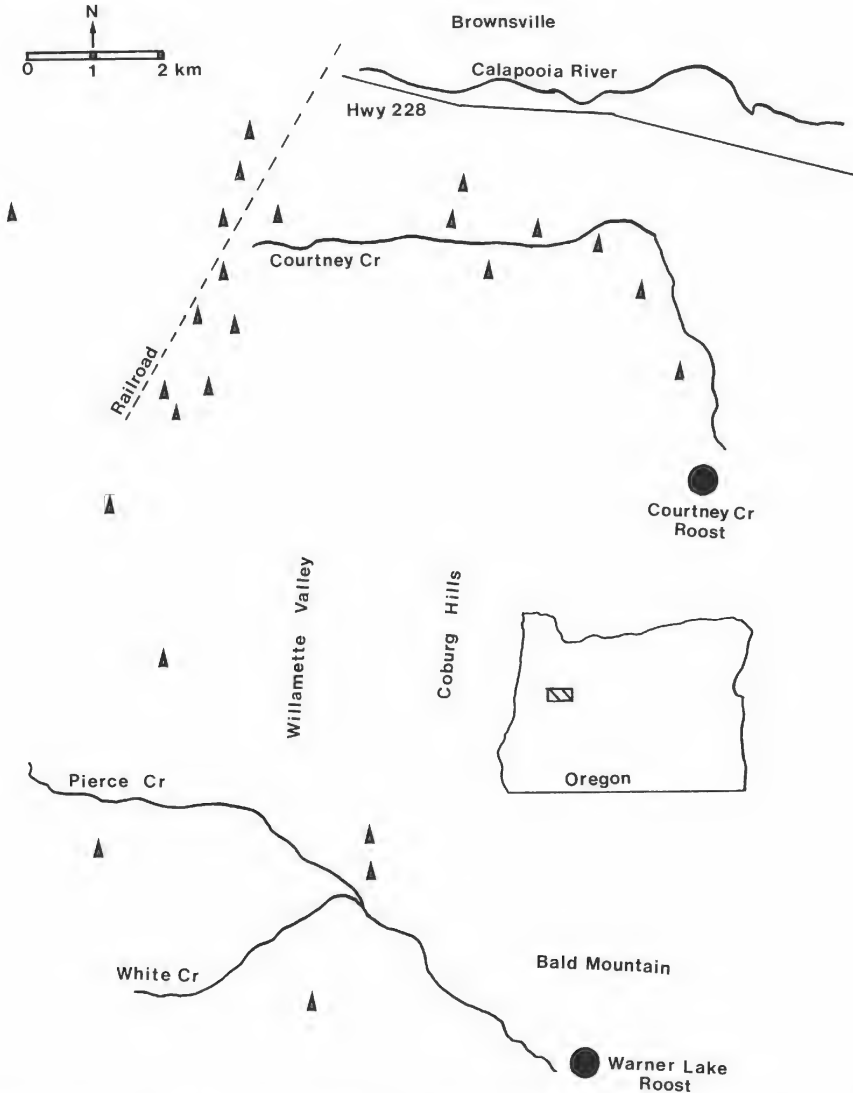


Figure 1. Location of foraging areas (triangles) with at least five bald eagles sightings and roosting (circles) areas in the Willamette Valley, Oregon. Only foraging areas within 11 km of night roosts are shown.

years (local ranchers pers. comm.). Numbers of eagles using this area and their wintering diets have never been described.

Methods

Observations of bald eagles were made twice each week from December through March 1987 between 0800 and 1630 hours. Two observers searched for bald eagles by travelling all-weather roads within 20 km of known roost sites. Once eagles were located, observers watched them with 10 x binoculars and spotting scopes and recorded information on time of day, flight direction of eagles, behavior (i.e., flying, perched, feeding), distance to nearest road as determined from USGS topographical maps (1:24,000 scale), perch type and species, and prey (live sheep, afterbirth, sheep carrion). Whenever possible, eagles were identified as adults based on white heads and tails or subadults. Numbers of adults and subadults were expressed as the highest of two counts conducted each week.

Additional information on winter diets was obtained by examining the contents of 45 eagle castings collected from the base of roost trees. Brown (1976) indicated that eagle castings provide useful information on dietary habits of eagles but that they are not a quantitative technique for determining prey composition.

Results

Bald eagles were observed on the study area from 5 December to 25 March (Figure 2). During most of this period, subadults (68.2%) outnumbered adults (31.8%). Eagle numbers fluctuated throughout the observation period and peaked at 20 birds on 4 February. The peak count was followed by a decline in eagle numbers and no eagles were seen after 25 March (Figure 2).

A total of 32 observations of foraging bald eagles was made on the study area. Eagles fed exclusively on sheep carcasses and afterbirth but have also been observed feeding on fish in nearby streams (local ranchers pers. comm.). On five

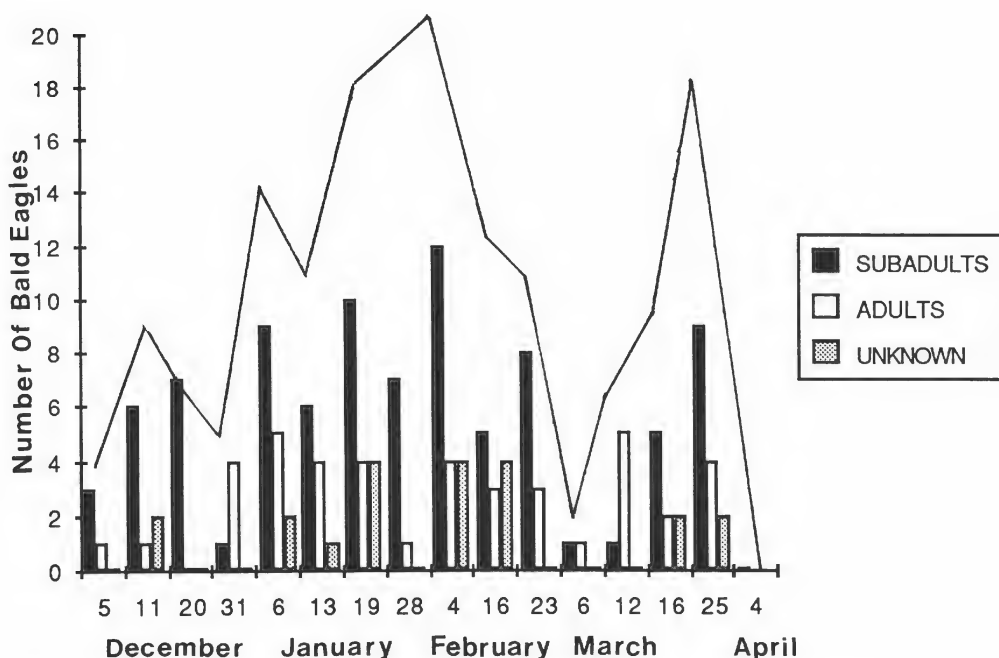


Figure 2. Numbers and age structure of bald eagles obtained from feeding ground counts in the Willamette Valley, Oregon, 1986-87. The line graph represents the highest total count for each week.

occasions, bald eagles were observed perched or feeding within 5 m of live lambs; however, no predation attempts on live lambs were observed.

Analysis of eagle castings indicated that domestic sheep was an important prey item and this is supported by our observations of foraging birds. Of 45 eagle castings collected at roost sites most were sheep remains (93.3%, $n = 42$) followed by waterfowl (4.4%, $n = 2$) and small rodents (2.2%, $n = 1$).

Eagles were most often observed feeding in pastures bordered by tall (> 20 m) cottonwoods. Primary feeding areas where eagles were seen at least five times occurred within $6.82 \text{ km} \pm \text{SE} = 0.53 \text{ km}$ ($n = 25$) of night roosts and no birds were observed beyond 13 km (see Figure 1). Most sightings of foraging birds occurred within 150 m of roads (Table 1). Because all our surveys were conducted from roads, this result was not surprising. However, only one adult was observed foraging or perched within 50 m of a road and all others occurred beyond this distance. Differences in adult and subadult foraging distances were significant ($X^2 = 16.3$, $df = 5$, $P < 0.01$). This difference suggests that adults were less tolerant of road traffic while feeding and is consistent with other studies (Stalmaster 1976, Isaacs pers. comm.)

TABLE 1. Distance of foraging bald eagles to nearest roads in the Willamette Valley, Oregon.

Distance (m) to nearest road	Subadults		Adults	
	n	%	n	%
< 10	13	27.1	0	0
10- 50	3	6.3	1	6.7
51-150	20	41.7	6	40.0
151-400	8	16.7	2	13.3
401-800	1	2.1	6	40.0
> 800	3	6.3	0	0

Discussion

Use of the Willamette Valley by bald eagles was related to availability of sheep carrion and after-birth. Peak concentrations of bald eagles coincided with the lambing period (i.e. early to mid-February) and the high proportion of subadults (68.2%) was probably related to an abundant supply of sheep carrion on the study area. Other

studies of wintering eagles in Oregon (Isaacs and Anthony 1987, Isaacs pers. comm., Keister *et al.* 1987) also indicate high concentrations of subadults when the food supply was abundant.

Sheep ranchers in the Willamette Valley typically move their sheep to different pastures before and after the lambing period to prevent overgrazing and starvation. Shifts in the location of preferred foraging and roosting areas of eagles coincided with these movements. Prior to 12 February, for example, sheep were abundant in pastures north and west of the Courtney Creek Roost (see Figure 1). Most foraging and roosting of eagles took place in this area which was near the majority of sheep pastures. However, after 12 February most of the sheep were moved south of this area and closest to the Warner Lake Roost. Foraging and roosting of bald eagles shifted to the Warner Lake Roost area following these sheep movements. Isaacs and Anthony (1987) report similar shifts in foraging locations by wintering eagles that coincided with changes in availability and location of cow carcasses.

Land-use changes have altered the Willamette Valley from a grassland, savannah and riparian mosaic (Towle 1979, Boyd 1985) to primarily an agricultural landscape. Such changes may have caused concomitant shifts in eagle diets. Although sheep carcasses were the major prey item consumed by eagles, dependency on this food base might increase the eagles' vulnerability to changes in agricultural practices. Moreover, past logging in the adjacent hills has reduced roosting habitat; most older-age forest has been removed during the past 50 years. Foraging habitat of bald eagles in the Willamette Valley should be protected from widespread changes in land-use and consideration given to remote areas where the birds can forage without human disturbance. Landowners should be encouraged to place sheep carcasses at least 150 m from nearby roads (1) to allow feeding by eagles of all ages, (2) to divert eagle use away from areas where they may be killed and (3) to provide winter food in an area that once supported a much larger and diverse prey base for this threatened species.

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Snow Avalanche-Dams and Resultant Hazards in Glacier National Park, Montana

Abstract

Snow avalanches form natural dams to creek and river flow in Glacier National Park, Montana. Dams are produced primarily by dense wet snow avalanches. Because such dams are unstable and so pose a serious threat to downstream habitats, I analyzed them in areas of Glacier National Park. Dam formation occurs under conditions of either zonal or meridional flow. Dams may be deposited during winters of high avalanche frequency, but such conditions are not essential. Temporary reservoirs have been impounded by avalanche-dams, causing stream impoundment and inundation of highways. Calculated potential maximum flood discharges illustrate a hazard of serious proportions, in some cases exceeding all but one known historical spring flood. Three areas in the Park are of special concern because of the history of avalanche-dam development across transportation lines. Future avalanche-dams and resultant outburst floods could damage roadways and a major bridge.

Introduction

Natural dams form in many ways. Barriers can be formed by landslides, ice or snow, glacial moraines, volcanic eruptions, fluvial deposition, eolian deposition, coastal sedimentation, and by organic accumulations (Costa and Schuster 1988). Most natural dams are inherently unstable, and dam failure can lead to widespread devastation and loss of life (Costa 1988).

Snow avalanches form natural dams in alpine environments around the world; outburst floods and associated devastation caused by failure of snow avalanche-dams have been reported from the Andes of Argentina (King 1934), the European Alps (Allix 1924, Peattie 1936, Tricart *et al.* 1961), the northern Scandinavian region (Rapp 1960), and the Torlesse Range of New Zealand (Ackroyd 1987). One such tragedy was described by Peattie (1936, p. 59): "On the 20th of February, 1720, the Swiss village of Obergestelen was destroyed and 84 of its 200 inhabitants were killed by an avalanche which leaped an intervening forest and wrecked one-third of the village. . . . The snow from the avalanche blocked the river Rhone, which quickly cut through it and then flooded a portion of the settlement." The failure of the avalanche dam and subsequent flooding exacerbated an already desperate situation, and occurred during recovery operations.

Despite the widespread occurrence of snow avalanches and avalanche accidents in Canada and the United States (Stetham and Schaerer 1979, 1980; Schaerer 1987; Williams and Armstrong 1984), there has been very little focus on

snow avalanche-dams and resultant floods in the mountainous regions of North America; exceptions include the study by Mokievsky-Zubok (1975) in an uninhabited portion of the Coast Mountain Range of British Columbia, and the recent work of Campbell (1988) in the vicinity of McBride and Valemount in the Robson Valley of British Columbia. As population pressure and mountain developments continue throughout the North American west, it becomes increasingly important to identify areas susceptible to potential flooding from snow avalanche-dam outbursts (Campbell 1988). The purpose of this paper is to describe the hazards associated with avalanche-dam failure and also to document the geographic extent and climatic characteristics responsible for the formation of snow avalanche-dams in a typical North American alpine environment.

Snow Avalanches and Avalanche-Dams

Two major types of snow avalanches are recognized in avalanche classifications: the slab avalanche, where a large area of cohesive snow across a slope begins to slide all at once; and loose snow avalanches, which start at a point or over a small area and increase in size as they descend (LaChapelle 1985, p. 19-20). Loose snow avalanches are frequently subdivided into dry snow and wet snow avalanches. Of these three types (slab, dry loose, and wet loose snow), wet snow avalanches are the primary mechanism for creating snow avalanche-dams. Slab avalanches frequently disintegrate into smaller masses upon descent (LaChapelle 1985), and dry loose snow avalanches frequently do not possess sufficient

cohesion to act as efficient dams. The wet snow avalanches, because of their weight and density, possess enough strength to temporarily dam creeks and rivers and create short-term natural reservoirs.

The period of time in which an avalanche-dam may exist will vary with the size, cohesiveness, and density of the snow deposit. Estimates of longevity of known avalanche-dams range from about one hour (Allix 1924) to over eight days (Mokievsky-Zubok 1975). One example of the density of a wet snow deposit which formed an avalanche-dam in the present study area is provided by Martinelli (1984). He examined an avalanche deposit which temporarily dammed the Middle Fork of the Flathead River in northwestern Montana. The deposit, examined four days after deposition, still had many large air spaces within and was composed largely of wet icy balls of snow. Debris density, measured with a Federal snow sampler, averaged 414 ± 37 kg/m³ for eight samples.

The Study Area

Glacier National Park, located in the Rocky Mountains of northwestern Montana, is typical of many North American alpine areas. Increasing winter usage of the Park for recreational purposes occurs in heavily glaciated terrain prone to snow avalanches. Major transportation links also pass through this avalanche-prone terrain (Figure 1). U.S. Highway Number 2 (US2) is a major east-west transportation link in Montana which parallels the Middle Fork of the Flathead River along the southernmost boundary of the Park (Figure 1). A daily average of at least 714 vehicles use this highway (Butler 1986b), which was completed through this area in 1930. The only road that penetrates deeply into, and crosses, the Park is Going-to-the-Sun (GS) Road, a narrow, two-lane road which was opened to traffic in 1933. GS Road usage is seasonal, typically open only from late May to late October. Avalanche potential is high along GS Road in winter and spring, and the avalanche paths which occur in this area penetrate through the mature forest to impinge upon the valley bottom (Butler 1980). McDonald Creek is a major permanent stream that parallels GS Road for about 10 km above the head of Lake McDonald.

The peak snow avalanche month in the Park is February, with secondary maxima in January

and March (Butler 1986a). Meteorological triggering mechanisms for avalanches there include: 1) heavy snow, 2) heavy snow followed by a rapid rise in temperature to above freezing, 3) a rise in air temperature to above freezing without precipitation, and 4) rain in association with above-freezing temperatures (Butler 1986a). Avalanche types present along the major transportation links include dry loose snow avalanches, wet snow avalanches, and slab avalanches (Butler and Malanson 1985a, 1985b, Butler 1986a, 1986b). Wet snow avalanches are the most common type to affect the major roads, with 80 percent of 223 studied avalanches resulting from weather conditions with temperatures above freezing (Butler 1986a, p.82). Wet snow avalanches are also the predominant type of avalanche in other regional study areas such as the Kananaskis region of southwestern Alberta (McPherson *et al.* 1984). Because wet snow avalanches are the primary avalanche type in the area, it is not surprising that a hazard exists from avalanche-dams and associated outburst floods.

Methodology

In recent studies of avalanche accidents in Glacier National Park, Butler (1986a, 1986b) compiled statistics on the location and nature of snow avalanche incidences for the 75-year period 1910-1985. Data sources included Glacier National Park Ranger daily logbook entries and monthly summary reports (Unpublished Monthly Ranger Report¹); U.S. Government monthly weather summaries for all years since 1910; unpublished letters, files, photographs, and slides on file in the Glacier National Park library; information from the Montana Department of Highways; and all December through May issues, 1946-1988, of the *Hungry Horse News*, a local weekly newspaper published since 1946 in Columbia Falls, Montana. This newspaper provides local accounts of avalanche occurrences of a size or timing significant enough to hinder local transportation and impact local tourism.

This study uses the same historical data set, and is supplemented by additional sources covering the winters of 1985-1988. Information was recorded on the location of snow avalanche dams, weather conditions associated with the avalanching, and the type of avalanche which formed

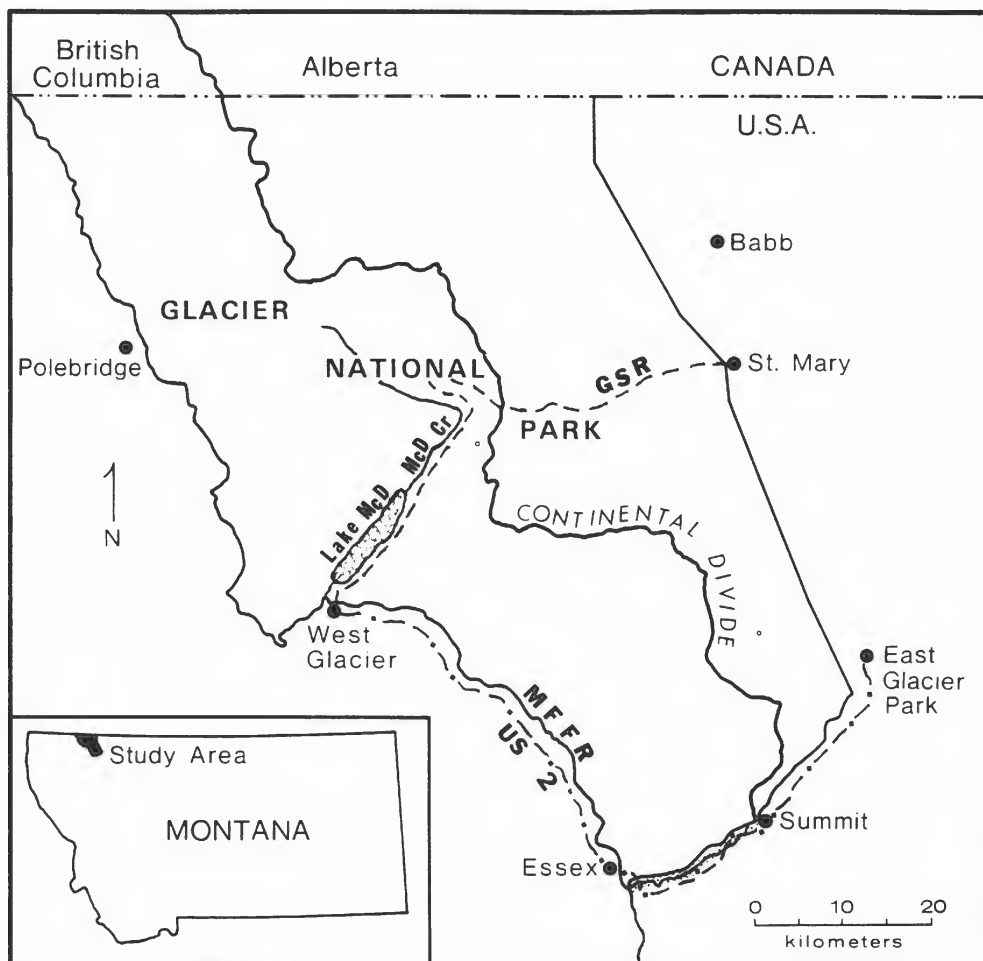


Figure 1. Locations susceptible to avalanche-dam hazards, Glacier National Park, Montana. Abbreviations as follows: GSR, Going-to-the-Sun Road; US2, U.S. Highway 2; MFFR, Middle Fork of the Flathead River; McD Cr, McDonald Creek; Lake McD, Lake McDonald. Shaded area west of Summit is Bear Creek. Small open circles, other dam sites.

the dam. Dam longevity and damage caused by dam formation and subsequent failure were also recorded. The area of avalanche-dammed reservoirs was delineated (based on historical descriptions), plotted on 1:24,000 scale topographic maps, and multiplied by depth of inundation to derive rudimentary volume estimates. Because no empirically-derived formula exists for calculating peak discharge of floods from avalanche-dam failure, estimates were calculated using the methods of Clague and Mathews (1973), and

Costa (1988), designed for use with jökulhlaups. These formula relate peak potential discharge (Q_{max}) to reservoir volume (V) based on known historical outburst floods.

Results

Years of Avalanche-Dam Formation

Since Park establishment in 1910, major snow avalanches have been numerous and geographically widespread in 1910, 1929, 1933,

1936, 1939, 1945, 1950, 1952, 1954, 1956, 1957, 1963, 1972, 1975, 1979, 1982, and 1986 (Butler 1986a, 1986b). Discounting those years prior to construction of transportation links, seven of fifteen major avalanche years have also produced hazardous snow avalanche-dams (number of dams in parentheses): 1933 (1), 1939 (2), 1952 (1), 1954 (3), 1956 (3), 1979 (1), and 1982 (1). Avalanche-dams have also been deposited during winters not particularly recognized as major hazard years for snow avalanching; these years include 1935, 1951, 1960, 1970, and 1984, each with one avalanche-dam occurrence recorded in Park and local records.

Location of Snow Avalanche-Dams

Avalanche-dam formation and the associated hazards are concentrated in three locations in Glacier Park (Figure 1): along McDonald Creek, from the head of McDonald Lake to the base of the Garden Wall²; along Bear Creek on the southern boundary of the Park³; and along the Middle Fork of the Flathead River near the southern tip of the Park⁴ (Figure 1). The latter two locations experience avalanches which disrupt traffic along U.S. Highway 2, whereas the former creates conditions damaging to Going-to-the-Sun Road. Two other reported cases from more isolated parts of the Park are also illustrated in Figure 1.⁵

There is no preferred slope direction associated with the formation of avalanche-dams. The avalanches in the Bear Creek area form on south to southeast-facing slopes, those along the Middle Fork of the Flathead form on southwest-facing slopes, and those along McDonald Creek develop on west- to northwest-facing slopes.

Meteorological Conditions Associated with Avalanche-Dam Formation

Precise temperature and precipitation data are not available from avalanche paths in Glacier National Park. However, general statements describing weather conditions and types of avalanche deposits provide some insight into local meteorological conditions during avalanche-dam deposition.

Of the known incidences of avalanche-dam deposition, 59 percent were a result of wet snow avalanches occurring while air temperature was above freezing. This conclusion is not unex-

pected, given the preponderance of wet snow avalanches in the overall pattern of avalanche types in Glacier Park (Butler 1986a). The remaining 41 percent have little data available for determining type of avalanche and meteorological conditions. The main exception is the deposition of a powder snow dam during a blizzard in 1956, when over two feet (60 cm) of new loose snow was deposited in a period of a few hours.⁶ Another dam was deposited in late January 1960 after an unusually heavy snowfall. Temperatures at this time were below freezing.⁷

The patterns of atmospheric flow conducive to major avalanche winters in Glacier National Park have been described by Butler (1986a). Briefly, two alternative synoptic patterns exist which have produced major avalanche cycles in the Park: winters with strong zonal flow, heavy snowfall, and rapidly fluctuating temperatures; and winters with sustained meridional flow and catastrophic avalanching resulting from subsequent invasion and advection of Pacific air. These patterns were shown to be similar to those affecting the Rogers Pass area of British Columbia as described by Fitzharris and Schaerer (1980).

A comparison of years of high frequency avalanching with years in which many avalanche dams were produced reveals that both atmospheric flow-patterns can produce avalanche dams. The winters of 1933 and 1954, for example, were years of strong zonal flow and avalanche-dam deposition; but, the winter of 1979 was strongly meridional in nature and also led to dam production. The key to efficient avalanche-dam development is apparently not so much the overall flow pattern as it is the tendency for warm (above freezing) temperatures and wet snow avalanche occurrence.

Avalanche-Dam Damage and Potential Hazards in Glacier Park

Deposition of avalanche-dams has produced temporary road blockages in and along the boundaries of the Park, as temporary ponds or redirected streams have covered the highways. These blockages produce unaccounted but distinct financial losses for businesses located along Highway 2.

An avalanche-dam deposited in April 1952 blocked McDonald Creek and completely redirected the stream onto the surface of GS Road. The highway was completely soaked, and the springtime snow removal had to be delayed until the road dried out and could bear the weight of heavy snow-clearing equipment.⁸ Past blockages of Bear Creek along the southern border of the Park have also temporarily caused submergence of Highway 2.⁹ Future occurrences of avalanche-dams along these creeks will undoubtedly lead to similar situations.

Estimated peak discharges ($Q_{\max}$) of past outburst floods vary by location. Estimated $Q_{\max}$ values along Bear Creek range from 39 cubic meters per second (cms) utilizing Clague and Mathews' (1973) equation, $Q_{\max} = 0.0075 V_{\max}^{0.67}$, to about 59 cms using the Costa and Schuster (1988) equation ($Q_{\max} = 113 V^{0.64}$, with V in 10^6 m^3 format). Application of the same formulae produces ranges of 56 cms (Clague and Mathews 1973) to about 105 cms (Costa and Schuster 1988) for both McDonald Creek and the Middle Fork of the Flathead River. The Bear Creek value exceeds all historical spring flood discharges except for the catastrophic June 1964 flood (more than 300 cms; Boner and Stermitz 1967). Prior to 1964, the maximum spring discharge flood along Bear Creek was less than 25 cms, a value exceeded by estimated avalanche flood outbursts. Calculated avalanche outburst discharges do not approach the historical maximum of greater than 2500 cms (June 1964; Boner and Stermitz 1967) along the Middle Fork and in excess of 700 cms along McDonald Creek above Lake McDonald. Nevertheless, the avalanche discharge values for these latter two streams may occur approximately once every 3-5 years, whereas the extreme maximum spring flood values appear but infrequently in the historical record. It is not out of the question for more than one avalanche-outburst flood to occur at one location in one winter, if several temporary avalanche-dams develop in the same location and subsequently fail.

Several past avalanches have delivered large quantities of downed timber to the damming deposit.¹⁰ This timber can act to anchor and stabilize the snow dam, prolonging its longevity and therefore increasing the size of the temporary reservoir upstream. Upon the inevitable failure of the dam, a greater flood is unleashed

which also contains large pieces of timber that act as battering rams along stream banks and at bridge abutments. The past blockages of the Middle Fork of the Flathead River have included large quantities of timber, suggesting the future possibility of a dam efficient enough to produce an outburst flood of sufficient size to damage the highway bridge where US2 leaves Glacier Park and enters the small community of Essex (Figure 1). Destruction of a highway bridge by direct avalanche impact in 1979 caused a month-long closure of US2 and necessitated a 300 km detour; similar impacts would be felt if the bridge spanning the Middle Fork is damaged or destroyed by an avalanche-dam outburst flood.

Conclusions and Recommendations

Avalanches made of wet loose snow are most likely to produce snow avalanche-dams in Glacier National Park. No preferred slope orientation exists for the occurrence of avalanches which produce dams. Avalanche-dams have developed along McDonald Creek, Bear Creek, and the Middle Fork of the Flathead River, under synoptic conditions of both zonal and meridional flow. Avalanche-dams have dammed reservoirs which temporarily inundate transportation lines in and adjacent to the Park. Calculated volume estimates and peak discharges from avalanche-dam reservoir formation and failure provide mute testament to the destructive capabilities of these natural hazards. Potential exists for outburst floods from avalanche-dams which could destroy highway transportation along the southern edge of the Park. Future avalanche-dams and resultant hazards in the area are likely. As has been shown elsewhere (Butler 1987) local residents who frequently drive on US2 are largely unaware of the extent of the snow avalanche hazard in the area. It is likely that future avalanche-dam outburst floods could produce serious damages and possible loss of life.

The National Park Service and Montana Department of Highways should be made aware of these potential hazards, and road-crew employees should be cognizant of conditions conducive to dam formation and failure. Because of the nature of its mission, the National Park Service is unlikely to engage in any widespread engineering practices within the Park along McDonald Creek to mitigate the hazard. Rather,

monitoring and temporary road closures will probably be the most cost-effective method of dealing with the hazard during spring snow clearance. Little can be done to prevent avalanche deposits from damming Bear Creek and the Middle Fork, and few options exist for highway rerouting in the confines of the narrow canyons where the streams and highway parallel each other. Along U.S. 2, the Montana Department of Transportation should also anticipate weather conditions

conducive to dam development and outburst flooding, and prepare for temporary road closures during time of high risk.

Acknowledgments

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Notes

1. Unpublished Monthly Ranger Report, 1935, Lake McDonald Ranger report, March. Unpublished Monthly Ranger Report, 1939a, Glacier Natl. Park Chief Ranger Report, February. Unpublished Monthly Ranger Report, 1939b, Lake McDonald Ranger Report, February. Unpublished Monthly Ranger Report, 1939c, Fish Creek Ranger Report, March. All on file at G. Ruhle Library, Glacier Natl. Park, West Glacier.
2. *Hungry Horse News*, 13 April 1951. Park moose ignores avalanche, plow, p. 1. *Hungry Horse News*, 11 April 1952. Snow slide causes creek to take over Going-to-the-Sun Highway, p. 1. *Hungry Horse News*, 16 April 1954. Sun Highway to Avalanche open, p. 1. *Hungry Horse News*, 10 April 1970. Avalanche off Mt Cannon in Glacier National Park is deeper, p. 12. *Hungry Horse News*, 5 April 1984. Snow barrier, p. 1. *Hungry Horse News*, 12 April 1984. Snow and ice from Going-to-the-Sun Road float down McDonald Creek in Glacier National Park, p. 1.

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3. *Hungry Horse News*, 27 January 1950. Report about snow slides from Essex, p. 5. *Hungry Horse News*, 2 March 1956a. Avalanche blocks G.N. and No. 2, p. 1.

4. *Hungry Horse News*, 2 March 1956b. Report increased snow depths in Glacier Park, p. 1. *Hungry Horse News*, 9 March 1956. U.S. No. 2 re-opening Saturday, p. 1. *Hungry Horse News*, 30 March 1956. Find snow depths just over normal, p. 1. *Hungry Horse News*, 25 February 1982. This time, the bridge held, p. 5. *Hungry Horse News*, 2 March 1956a, *op cit.*

5. *Hungry Horse News*, 23 April 1954. Park plows find record snow depth near Garden Wall, p. 1. *Hungry Horse News*, 21 May 1954. Avalanches cause park destruction, p. 1.

6. *Hungry Horse News*, 2 March 1956a, *op cit.*

7. *Hungry Horse News*, 5 February 1960. Here are 1960 avalanches in Glacier National Park, p. 10.

8. *Hungry Horse News*, 11 April 1952, *op cit.*

9. *Hungry Horse News*, 2 March 1956a, b, *op cit.*

10. *Hungry Horse News*, 9 March 1956, *op cit.*

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Spring and Summer Food Habits of Black Bears in the Pelly River Valley, Yukon

Abstract

Food habits of black bears (*Ursus americanus*) from the Pelly River Valley, Yukon, were examined to determine the seasonal importance of various foods for bears inhabiting a northern environment. Food habits were determined by analysis of 59 scats and one stomach. Herbaceous material and berries accounted for 95 percent of the scat volume during spring and summer. Horsetail (*Equisetum* spp.), bearberry (*Arctostaphylos uva-ursi*), soapberry (*Shepherdia canadensis*), and graminoids were the most important foods. Overwintered berries were eaten early in spring until herbaceous vegetation became available. New berries were important from mid to late-summer. Insects, particularly ants, were frequent in scats from May to August, but were only two percent of the total diet volume. Seasonal food habit information is important because it reflects seasonal trends in black bear habitat use. Food habit preferences of bears in northern environments are generally similar to those in southern areas; however the restricted availability of different foods limits diversity in northern diets.

Introduction

Food habit studies provide information about the relative importance of different foods to an animal's diet. For black bears (*Ursus americanus*), this information is important to understand their life history and help investigators assess the seasonal importance of different habitats. Habitat use has been shown to vary with the availability, distribution and abundance of preferred foods (Hatler 1967, Jonkel and Cowan 1971) and changes in the seasonal use of plant and animal foods by black bears is common (Penner *et al.* 1980). There is little information on the food habits of northern black bears (Hatler 1972). Information on the ecology of northern black bears is important for their effective management, particularly under the increasing encroachment of human development.

Food habit information was obtained in 1984 for black bears inhabiting the Pelly River Valley near Ross River, Yukon. My objectives were to determine the seasonal importance of various foods in the diet of black bears inhabiting a northern environment and to compare the diet of northern black bears with those in other areas.

Study Area

The study area is located along the Pelly River Valley (62°00'N, 133°30'W) and is representative of major river valleys in the southern Yukon. The area is traversed by the Robert Campbell Highway running east to west along the Pelly River, and the Canol Highway running

north along the Ross River and south along the Lapie River. The town of Ross River is located on the Canol Highway at the confluence of the Ross and Pelly Rivers.

The study area lies within the Pelly River Ecoregion (Oswald and Senyk 1977). It has mean annual temperatures ranging from -4°C to -7°C, with mean January temperatures of -27°C to -35°C and mean July temperatures of 13°C to 15°C. Valley bottoms have mean annual precipitation of between 250 and 300 mm.

The Pelly River Valley is dominated by white spruce (*Picea glauca*) forest on dry sites and black spruce (*Picea mariana*) forest on wetter sites. In white spruce forest, shaded sites are sparsely vegetated with mosses, horsetails (*Equisetum* spp.), and rose (*Rosa acicularis*). Where the canopy is open, willows (*Salix* spp.) are prevalent and there is a greater abundance of herbaceous vegetation. In black spruce forest there is moss ground cover with dense willows and ericaceous shrubs where the canopy is open. Steep south facing slopes rise several hundred feet above the Pelly River and are dominated by sagewort (*Artemisia* spp.) grassland. Aspen (*Populus tremuloides*) occurs in gullies that drain these hillsides. Aspen forest also occurs in burned over sites that are common in the southern portion of the study area.

Deciduous trees and shrubs on the study area flush by the end of May. Arctic lupine (*Lupinus arcticus*) is the first plant to flower in the spring followed by other perennials, vetch (*Astragalus*

spp.), locoweed (*Oxytropis* spp.), and lousewort (*Pedicularis* spp.). Major annuals such as horsetail appear in early to mid-June. Most plant species have flowered by the end of June. Frost occurs in mid-August which initiates the end of the growing season.

Methods

Scats from black bears were collected between 15 May and 20 August, 1984. All scats were labelled with date of collection and remarks on probable age. Scats were frozen until analysis in August of 1984 and 1985.

Scats were thawed and washed on a No. 18 sieve to remove fines. Sieve contents were mixed with water and distributed evenly in an enamel pan. A random 10 ml sample was removed from the pan, mixed with 30 ml of water, then put into a square petri dish and spread over a 25 square grid (i.e. each square = 4%). The percent volume of each item in the sample was estimated. Three to five samples were examined from each scat. Observations of feeding bears aided in the assessment of seasonal food habits.

Results and Discussion

The percent occurrence and average percent volume of identified contents were determined from 59 scats and one stomach (Table 1). Horsetail was the most frequent item in the samples and accounted for the greatest percent volume. Next in importance was bearberry (*Arctostaphylos uva-ursi*) fruit followed by soapberry (*Shepherdia canadensis*) fruit and graminoids. Animal matter, particularly ants and mammal hair, were frequently found in samples, but comprised a small percentage of the total volume.

To evaluate seasonal trends in food habits, collection dates were divided into two periods: spring, 28 May-30 June and summer, 1-30 July (Table 1). Only known aged scats ($\pm 1-2$ days) were used.

Bearberry fruits were common in the spring diet. In early May, 1984, many black bears were observed feeding on open south facing slopes above the floor of the Pelly River. They were likely feeding on overwintered bearberries and grasses because vernal growth did not occur on the slopes until late May. Graminoids and overwintered berries are common in the spring diet of black bears (McIlroy 1970, Jonkel and Cowan

TABLE 1. Percent occurrence (occ.) and mean percent volume (vol.) of food items in scat samples and one stomach from the Pelly River Valley, Yukon, 28 May-16 August, 1984.

Item	Spring 28 May- 30 June (n=17)		Summer 1 July- 30 July (n=31)		Total 28 May- 16 August (n=60)	
	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.
Herbaceous material:						
<i>Equisetum</i> sp.	70.6	50.4	32.3	28.5	48.3	39.1
Grasses	23.5	0.9	22.6	0.4	21.7	2.3
Unidentified	5.9	0.7	6.5	2.4	5.0	1.4
Other	0.0	0.0	6.5	1.9	3.3	1.0
Fruits:						
<i>Arctostaphylos uva-ursi</i>	52.9	27.4	25.8	9.8	33.3	15.9
<i>Shepherdia canadensis</i>	0.0	0.0	51.6	39.2	31.7	20.5
<i>Vaccinium vitis-idaea</i>	23.5	3.8	3.2	0.1	8.3	1.1
<i>Vaccinium uliginosum</i>	17.6	5.8	3.2	0.0	8.3	1.8
<i>Vaccinium</i> sp.	11.8	2.6	3.2	0.4	6.7	1.7
<i>Empetrum nigrum</i>	5.9	5.9	12.9	6.3	15.0	7.6
<i>Fragaria virginiana</i>	0.0	0.0	9.7	2.4	5.0	1.3
Unidentified	5.9	1.0	0.0	0.0	6.7	1.2
Ants	11.8	0.0	6.5	3.3	28.3	1.7
Other Insects	23.5	1.1	45.2	0.6	10.0	0.4
Vertebrate remains:						
Feathers	0.0	0.0	3.2	0.2	1.7	0.1
Hair	5.9	0.0	22.6	0.4	16.7	0.3
Bone	0.0	0.0	3.2	0.1	1.7	0.1
Forest litter	47.1	0.4	38.7	4.0	33.3	2.5
TOTAL		100.0		100.0		100.0

1971, Hatler 1972, Modafferi 1982, Smith 1984, Herrero 1985). Black bears lose energy between den emergence and the ripening of nutritious fruits (Jonkel and Cowan 1971, Rogers 1976, Beeman and Pelton 1980). Bears use overwintered berries in the spring because they are high in carbohydrates and because suitable herbaceous vegetation has not yet emerged (Herrero 1985). In the Pelly River study area, bearberries were the most common fruit in scats collected in the spring but they were supplemented by blueberries, bog cranberries, and occasionally crowberries. By early June vernal growth had begun in the valley bottom and the use of open slopes declined; however some black bears were observed on open slopes until late-July. The

continued use of the slopes coincided with the presence of bearberry in scats until mid-July. Insects, particularly ants, were the most frequent animal food during June and July. Similar trends are reported elsewhere (Chatelain 1950, Tisch 1961, Hatler 1972, Nagy and Russell 1978). Horsetail increased in the diet in the spring and summer corresponding with black bear movement to the valley bottom. Horsetail is common in the spring diet of black bears elsewhere (McIlroy 1970, Hatler 1972, Nagy and Russell 1978).

After mid-summer, soapberries were a major food until frost occurred and berries began to fall off the plants. Crowberry fruit occurred more frequently in the black bear diet as the summer progressed. Crowberry fruit comprised 48 percent of the volume of one stomach collected on 13 August and 73 percent of the volume of a scat collected on 16 August. In other north temperate and boreal forest areas, blueberries are a critical black bear food in late summer and early fall (McIlroy 1970, Jonkel and Cowan 1971, Hatler 1972, Rogers 1976, Modafferi 1982). In the Pelly River study area, blueberries were only common in scats during the spring but likely became more prevalent in the diet in August after scat collection ceased. Blueberry and crowberry are scarce in the Pelly River Valley near Ross River, but are common in subalpine areas to the north and

south. I suspect black bears disperse to these areas in the late summer when blueberry and crowberry fruits ripen. Qualitative evaluations suggest 1984 was a moderate to poor year for blueberry and bearberry production.

The results of this study cover only one year of collection, so they do not take into account year-to-year fluctuations in the availability of important foods, particularly berries. The results are expected to reflect the general trend in black bear food habits, however. Food habits over the sampling period are consistent with those found in other studies. Herbaceous foods are used early in the summer, fruit is added as it becomes available and animals (usually insects) are used opportunistically during summer (Hatler 1972, Penner *et al.* 1980). Food preferences of black bears in northern habitats are generally similar to those in southern areas; however, the restricted availability of different foods limits diversity in northern diets.

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W-Waves and Plant Communication

Abstract

Plants have been found to communicate directly with each other. An ax chop to one tree has been detected in a neighboring tree for example. The basis of this communication has been hypothesized to be W-wave signals.

Introduction

There is much recent research that suggests plants are able to communicate. Under stress, such as from insect attack, plants are hypothesized to emit chemical substances, pheromones, that, it is hypothesized, stimulate the surrounding plants to prepare to resist a similar attack (Rhoades 1985).

Earlier we reported the discovery of W-waves in plants (Wagner 1988a,b). Evidence for their existence consisted of measured electrical patterns, recorded oscillations, excitation behavior, and reflection phenomena. Measured electrical patterns appeared to indicate that standing waves are always present in plants and have something to do with their physiology. Recorded oscillations demonstrated another feature that one would expect to find if waves were present. Other evidence indicated that the observed waves were not electromagnetic but they interacted weakly with charge so it was possible to observe some of their effects with ordinary electrical measurement equipment. We found that one could disturb the apparent standing wave pattern in a tree at different locations and detect oscillatory behavior coming from two probes elsewhere in the tree. This would be typical behavior for disturbing a standing wave pattern anywhere. Using pulse reflections we found the velocity of the waves in the tree. The evidence all pointed to the existence of waves in plants.

We hypothesized that if insect damage caused trees to communicate maybe damage with an ax or nail would cause the tree to send an immediate message to the surrounding trees. The evidence given here seems to indicate that this is the case. We already knew that such mechanical trauma produced changes in the standing wave pattern in the damaged tree itself. We theorized that the W-waves involved could also

propagate through space or ground to adjacent trees (Wagner 1988a, 1989f). The purpose of this paper is to further discuss the evidence that suggests that W-waves are involved in this communication between plants.

Materials and Methods

Live Tree Samples

Much of the methodology is described elsewhere (Wagner 1988b, 1989h).

To determine if a live tree responded to stress damage to a neighboring tree we placed probes in a "transmitting tree" and in one or more "receiving trees." Every lead was grounded coaxial cable. Pairs of probes in receiving trees were spaced at varying distances to optimize the signal strength of the received signals. Trees with relatively few and smaller lower branches seemed to work best. Since we are dealing with wave phenomena that setup differently in each tree it is difficult to determine ahead of time the appropriate placement of contacts or exactly where one should chop to produce an optimum pulse. It was often effective to place the lower of the two probes on receiving trees just a few centimeters above the ground. Probes on transmitting trees usually used the standard two probe spacing (Wagner 1988b). Next the transmitting tree was chopped, struck with the sharp edge of a woodcutter's ax, near its base one to three times and the resultant signal simultaneously recorded from both the transmitting and receiving trees. Where two receiving trees were used, only the signals from the receiving trees were recorded because a two channel strip chart recorder was available at the time. Each channel was electrically isolated from the other one. A dry cell operated offset adjustable preamplifier was used in each channel. Attempts were made to minimize unnecessary disturbances to all plants near and

involved in the experiments since any kind of damage seemed to increase the electrical noise output levels of the trees involved in the experiments.

To obtain velocities of disturbances traveling between trees we used three trees. Table 1 shows results for both two-tree and three-tree experiments. Since W-wave disturbances seem to travel at approximately 1 m/sec in plant material (Wagner 1988a,b; 1989h), the processing time (the time the wave takes to spread within the sending and receiving trees before passing sensory probes) may vary with tree height and position of probes. To reduce the possible variation to effects of processing time, we reasoned that the use of two receiving trees of near equal heights with equally spaced probes and using the difference in arrival times of the transmitted signals would eliminate the possible delay variables (assuming the receiving tree delays are equal). When using three trees, one was chosen as a transmitting tree and the others as receiving trees. Following a chop into the transmitting tree a sharp rise (here termed a "pulse" for descriptive convenience) appeared in the output voltage first in the transmitting tree then in the receiving trees. The pulse arrival times were used, together with the difference in distances from the transmitting tree, to calculate the velocity of W-waves traveling between trees. Communication data were taken spanning more than a year in time, with variations in methods, to assure that the observed phenomena are real. Measurements were taken in trees at about 460 m above sea level.

Capacitor Sensors

To directly record W-waves, capacitors were used (Wagner 1989a,c,j). In preliminary results, capacitors connected to high impedance voltmeters have been observed to produce comparatively large fluctuating voltages. We attribute these fluctuations to W-waves in space (e.g. a 2 microfarad capacitor has been observed to produce as large as ± 50 mv fluctuations (unpublished observation)). We reasoned then that large volume capacitors would present a large cross section to W-waves. Thus we used them to monitor W-waves traveling in air between trees. Signals from these were analyzed on a Schlumberger model 1201 FFT low frequency spectrum analyzer. A differential input setting was used on the analyzer to minimize common mode signals. Two sensor

capacitors were made of Celotex, a foam type insulating material comprised of foam separating foil layers by 3.81 cm (1.5 in). One of the sensors was 96.5 cm x 50.8 cm (#1), and the other was 243.8 cm x 25.4 cm (#2). The capacitors were placed flat on level platforms, 1.52 m above the ground, made of two inch PVC pipe attached (by ropes) to trees in clumps of predominantly white fir (*Abies concolor*) (#1) and in madrone (*Arbutus menziesii*) (#2). Many precautions, to minimize noise, were followed when using the spectrum analyzer (see Wagner 1989h).

Salt Solution Saturated Tree Sections

To demonstrate that W-waves arise from external sources and that these waves are not peculiar to living organisms we used sections of trees filled with salt solution for communication experiments. Salt solution filled samples were prepared by placing 2.4 meter (or less) sections of freshly debarked live trees into 10 cm (4.0 inch) diameter PVC pipe filled with saturated salt solution. Then the end was capped. The container was then laid on its side for at least a month to allow the wood to absorb the salt solution. Salt solution filled samples were removed from the PVC pipe and tested on a wooden table in the laboratory.

Results

Live Tree Transmissions

Figure 1 shows the response of two ponderosa pines to three ax chops in quick succession (within 5 seconds) to the base of the transmitting tree. The two trees were about 13.7 m apart and both were approximately 28 cm in diameter at the base, and 9 m high. To assure a large amplitude transmitted pulse three ax chops were delivered. Further, not every chop gives a good response because it cannot be known ahead of time where exactly to strike the tree for maximum response because of the differences in the wave structure within different trees. Delivering more ax chops instead of one often makes the leading edge and other portions of the damage curve more complex than that for just one chop. For example, there are extra bumps after the start of the sharp rise in Figure 1. In Table 1 are shown some other results of 8 experiments. One chop or more was followed by a response in a nearby tree. In the earliest two cases (Table 1) we tested pairs of madrones. The damage curves

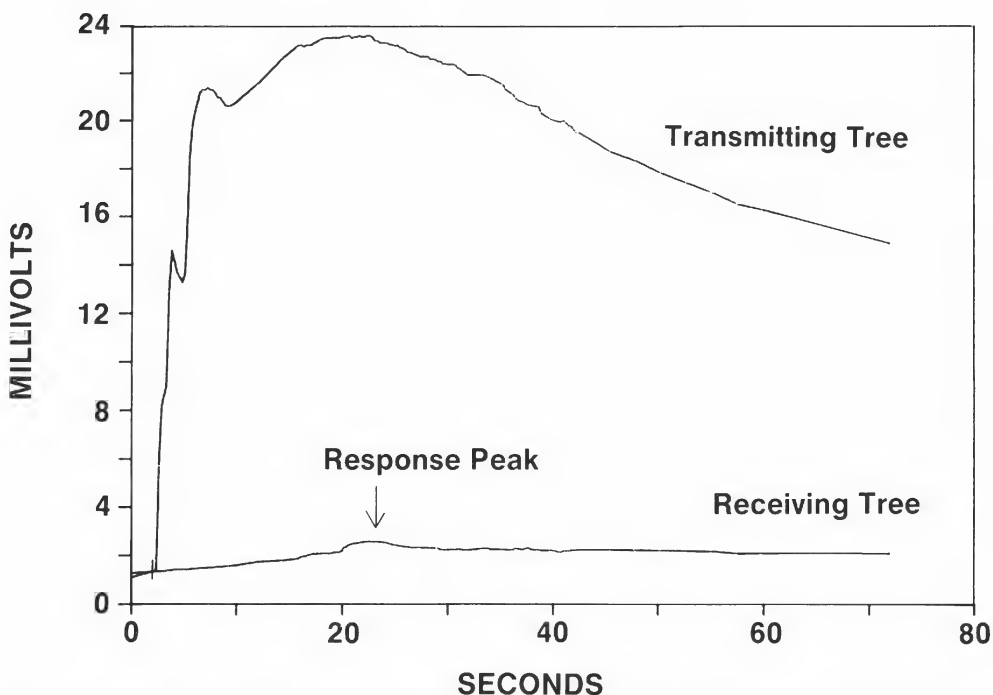


Figure 1. Transmitting and receiving tree responses to ax chops to the base of the transmitting tree. The higher curve is what has been previously designated a damage curve from chopping into the base of a tree. The lower curve represents the output of a receiving tree 13.7 m away. Note the rather small but sharp rise at about 20 seconds which is the beginning of the receiving tree response. The first chop occurred where the line crosses the curves just before the sharp rise.

are small in amplitude and the receiver responses close to 0.1 mV with receiver probe spacings of 1.5 m. These first results were enough to encourage further testing but we used larger receiver probe spacings (up to 7 m) with apparently somewhat larger amplitudes resulting. Due to the delays mentioned previously we did not use these initial experiments to determine a velocity for W-waves between trees but they still demonstrate that there is communication. The first 4 entries of Table 1 are typified by Figure 1. In Figure 1 the first chop occurred approximately at the time the small line crosses the two curves just before the sharp rise of the damage curve. The two curves are synchronized in time because the data from the strip chart recording (where the pens are displaced along the recording paper to prevent collision) was transferred point by point to a computer program which then replotted the curves. At about 20 seconds there

is a sharp rise (in some cases a dip, apparently depending on the wave pattern) in the receiving tree response indicating that the receiving tree has received data from the transmitting tree. From there the receiving tree response usually flattens (or begins oscillations or pulsations). In the meantime the damage curve from the transmitting tree is decaying rapidly.

It is difficult to obtain a second set of good data from trees in the vicinity immediately after finishing an experiment, where chopping is involved due to the noise (oscillations and changing voltages coming from probes) generated in the chopped and nearby trees. We usually attempted to obtain immediate second sets of data but often without success. The noisy condition persists for a few hours and then tests can be resumed.

Figure 2 shows the response of two receiving trees taken from a strip chart recording.

TABLE 1. These are results from some of the experiments done here relative to plant communication.

Date Temp.	Trans/Rec. Separation (m)	Ampl. Trans. (mv)	Ampl. Rec. (mv)	Delay (secs)	Vel. (m/sec)	Comments
3/18/88* 19°C	28.6	12.5	0.3	13	N/A	p. pine
3/17/88* 23°C	13.7	23.5	0.5	18	N/A	Figure 1
3/8/88* 17°C	2.1	10.0	0.1	3.6	N/A	First (madrone)
3/9/88* 7°C	4.9	2.0	0.1	10	N/A	madrone
3/31/88** 16°C	14.0	N/A	0.3	4.2	4.9	Figure 2 pine
	34.4		0.2			
4/1/88** 24°C	17.6	N/A	0.3	3.6	4.9	ash trans.
	35.4		0.1			
4/1/88** 25°C	7.3	N/A	0.1	5.6	4.6	ash trans.
	33.2		0.1			
4/5/88**	5.2	N/A	0.2	5.3	5.0	pine temp. not rec.
	31.7		0.1			

* The results from chopping at the base of a transmitting tree and one receiving tree.

** Data from sets of three trees where only the receiving trees were monitored while the transmitting tree was chopped. In the last four sets the delay is the time between the pulses received from the two receiving trees. The velocity of W-waves between trees is calculated by dividing the difference in distances from the transmitting tree by this delay. The species of trees used in these experiments were ponderosa pine (*Pinus ponderosa*), Oregon ash (*Fraxinus latifolia*), and madrone (*Arbutus menziesii*). The time for these experiments was between 0900 and 1700 hours. See the text.

These curves are illustrative of the second set of four entries of Table 1. Using 20.4 m for the difference in distance of the receiving trees from the transmitting tree and dividing by 4.2 seconds (the time between the sharp rises of Figure 2) gives 4.9 m/sec for the W-wave velocity between trees in this case. See Table 1 for other results. The average velocity obtained from the values in the table is 4.9 cm/sec for W-waves traveling between trees. The same procedure was used for the three last entries for determining the velocity of W-waves between trees.

Much additional data were taken to be sure of the communication result. Some of the additional data had relatively large receiving tree amplitudes some of which are: 0.6, 0.6, 0.3, 0.2, 0.8, and 0.4 mv. The corresponding distances of separation between receiving and transmitting trees were near 15.2, 13.1, 20.4, 21.6, 13.0, and

13.7 m respectively. These data were from ponderosa pine pairs.

Capacitor Signals

The very existence of apparent plant spectra from the large area capacitor sensors in the vicinity of trees seem to indicate that W-waves travel in air rather than through the earth alone since these sensors are in air with no direct connection to trees. These sensors when connected to the 1201 usually showed a 1.6 Hz series of harmonics plus some other peaks (Figure 3) that apparently are plant related since they seem to show only in the vicinity of a relatively high concentration of live plants and may indicate a constant communication between plants. They are found with much more detail when the spectrum analyzer is connected directly to plants (Wagner 1988a; 1989b,d, e,g,h,i,j). The data here may indicate some kind of W-wave resonance phenomena in plants.

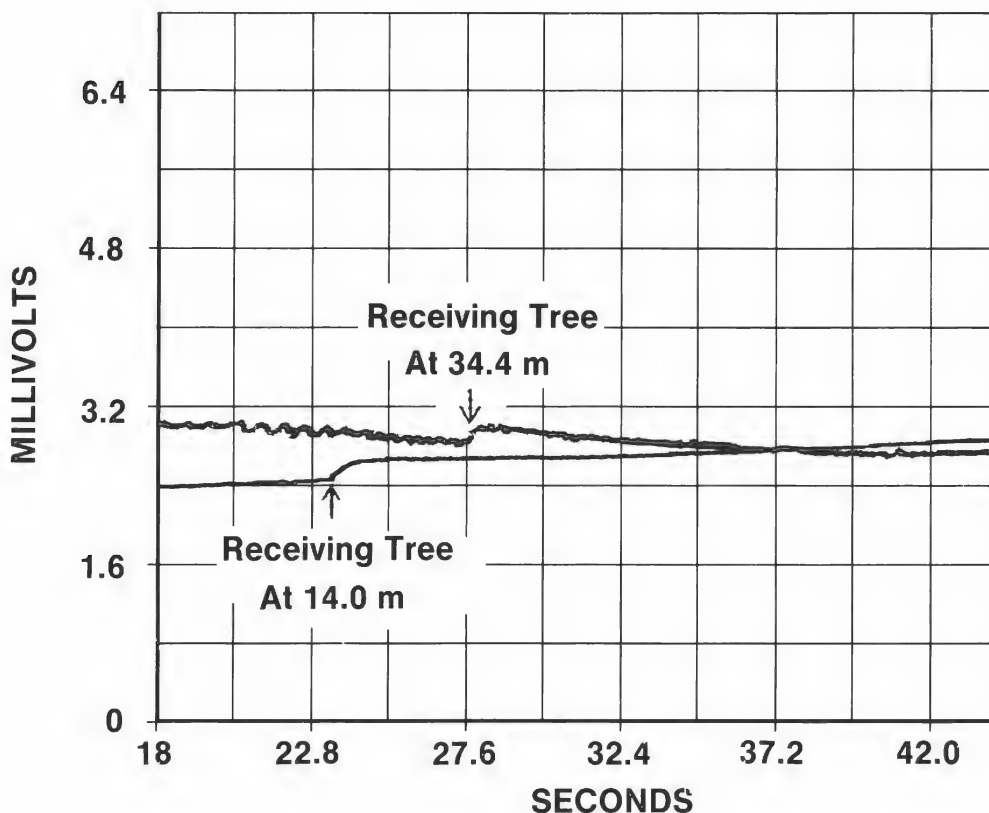


Figure 2. Curves of a strip chart recording of the response of two receiving trees to a woodcutters ax chop to a transmitting tree. The time on the abscissa is the approximate time from the ax chop. All three trees were ponderosa pine (*Pinus ponderosa*) near 10 m in height. See the text for more discussion and Table 1 for more data.

Salt Solution Filled Tree Sections

Attempts have been made to demonstrate communication between salt solution filled tree sections. So far the results have been ambiguous due to noise. This might be expected since wave patterns observed in salt solution filled tree sections have smaller amplitudes (compare Figure 4 with pattern data of Wagner 1988b). Also signals that are transmitted along salt solution filled tree sections appear to be weaker than comparable signals in trees (compare, for example, Figure 5 with Figure 1 the top curve). Thus probably transmitted signals would also be weaker.

Discussion

Characteristics of W-waves

W-waves seem to be distinct from electromagnetic waves. Some of the apparent characteristics of W-waves are as follows:

(1) W-waves appear to travel very slowly; at about 96 cm/sec in live plants (Wagner 1988a; 1989h,c) and here we find that they seem to travel at about 4.9 m/sec in air (the range was 4.6-5.0 m/sec). This is not characteristic of electromagnetic waves which travel at about 3.0×10^8 m/sec.

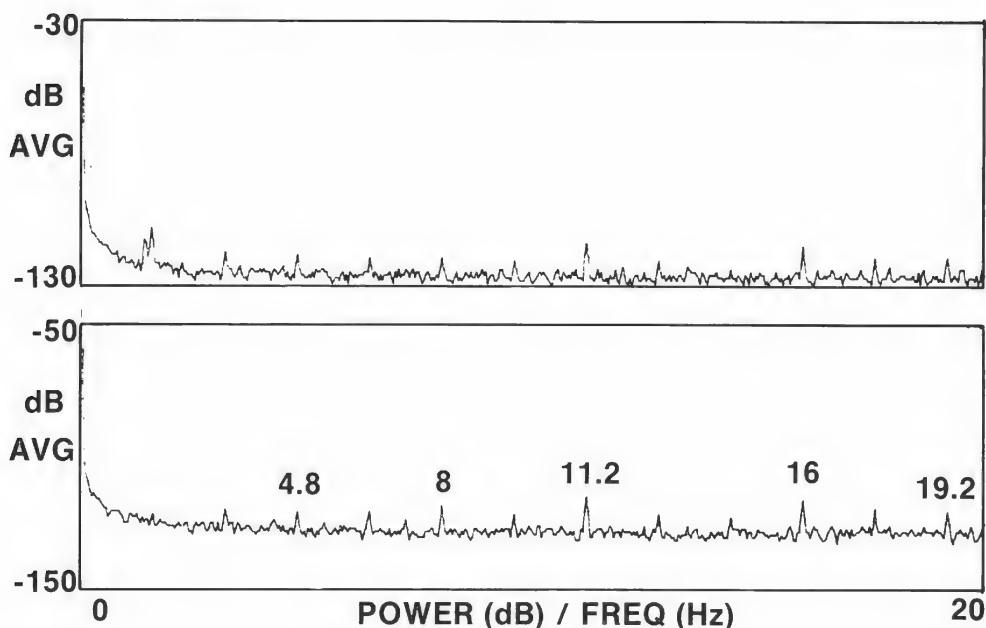


Figure 3. Typical spectra from the two different capacitor sensors that were used. The upper spectrum was from #1 and the lower from #2 (see the text). Some of the major peaks are marked with frequency (Hz). Other peaks can be identified by the fact that major peaks are spaced by 1.6 Hz. These spectra are present most of the time when the sensors are near plants, apparently indicating a W-wave field in the space near plants.

(2) A W-wave disturbance typically seems to produce a semipermanent displacement of charge (e.g. damage curve (Wagner 1988b) and Figures 1, 2, and 5 as indicated by the voltage changes) with a relatively slow decay of this displacement back to equilibrium. A typical electromagnetic pulse, however, is a quick change in voltage with a quick return to the original value. The W-wave behavior may be analogous to a light pulse falling on a semiconductor which produces excess minority carriers and then these slowly recombine with majority carriers in an exponential manner.

(3) W-waves appear to interact weakly with charge so that it takes appreciable time to build up charge (Wagner 1988b).

(4) A spectrum analyzer shows that characteristic W-wave frequencies often appear to combine (heterodyne; see e.g. Halliday et al. 1970 pp. 332-334) to form sum and difference frequencies with the frequency (f) of a small ac voltage applied with two probes along a plant stem (Figure 6). For example if f_1 is a proper (as yet we don't know what

determines which W-wave frequencies will combine with the ac signal) W-wave frequency then $f + f_1$ will appear in the spectrum as well as $f - f_1$. The analyzed signal is monitored from additional probes placed between the probes furnishing the ac voltage. The observed sum and difference frequencies appear to provide dramatic evidence for the existence of W-waves because their amplitudes are so large (can be millivolts) and the frequencies obtained (f_1) match those obtained from ordinary spectra as well as those obtained from plant spacings (Wagner 1988a; 1989b,g,h).

(5) W-waves seem to be a factor in the spacing of plant structures as the spacings when converted to frequency appear to match frequencies measured on the spectrum analyzer (Wagner 1989b,c,g,h). This appears to demonstrate standing wave action within a conducting medium where electromagnetic waves would quickly decay.

(6) W-waves seem to come from an external source since the set of frequencies obtained seems to be the same from every source. Concern that

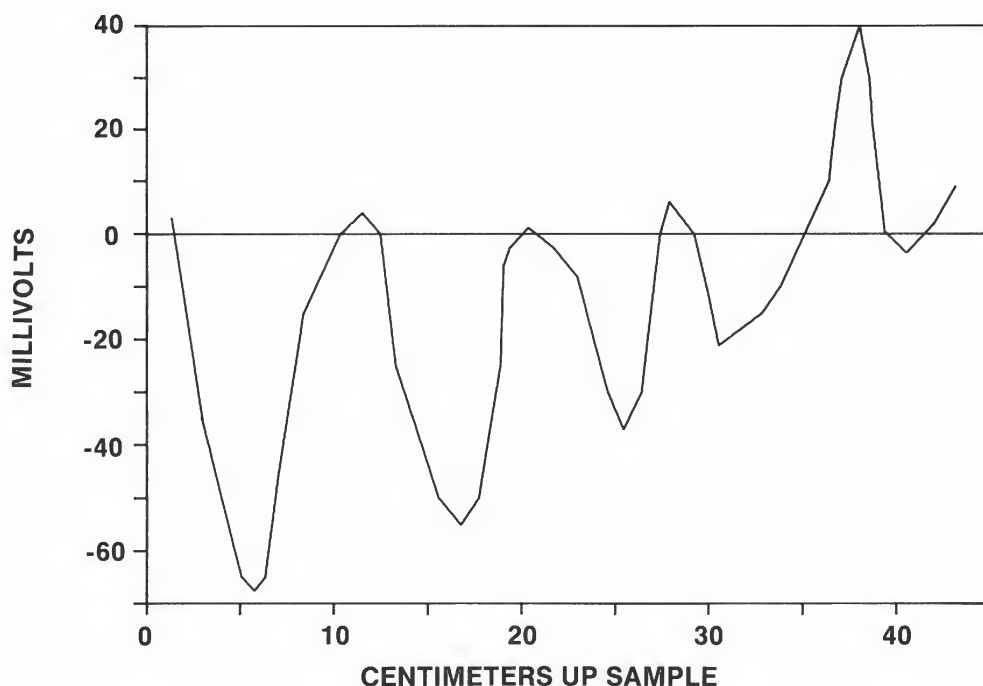


Figure 4. Wave pattern taken from a portion of a salt solution filled section from willow (*Salix* sp.). It was 3.5 cm in diameter at the base and 94 cm long. Probes were spaced at 1.25 cm. The amplitudes of peaks are considerably smaller than amplitudes usually obtained from live trees.

the spectra might be induced by external noise are addressed by noting that the spectra are nearly identical from experiments conducted on trees in different locations. Tests also indicate that they don't come from the equipment (Wagner 1989h). Thus W-waves (or whatever produces their frequencies in W-wave sensors such as plants, salt solution filled tree sections, and capacitor sensors) appear to be matter penetrating. For example they appear to travel in plants and highly conducting salt filled samples, and their spectra appear coming from either plants or salt solution filled samples located in metal shields (Figure 7; Wagner 1989d,e,i,j). Also we obtained characteristic spectra from a potted lemon tree located more than 100 m underground in a mine shaft (Figure 8). Such matter penetrating behavior is not characteristic of electromagnetic waves. The matter penetrating quality correlates with the fact that other plant phenomena appear to work anywhere on and in the earth (e.g. Salisbury et al. 1969 pp. 550-552).

Most of the above characteristics and others (see Wagner 1988b) are not typical of electromagnetic behavior and thus we believe that W-waves are a real and separate entity but they do seem to interact with charge and electromagnetic waves in a manner which is not completely understood at this time. The curves in Figures 1 and 2 look typical of W-wave behavior with, for example, their buildup and decay characteristics and the small velocities obtained and thus we associate the observed communication behavior with W-waves.

Live Tree Transmissions

Figure 1 shows considerable time delay between the initial response from the transmitting tree and the overt response of the receiving tree (at about 20 seconds). This time lag is apparently larger than just the transmission time perhaps due to the low velocity (approx. 1 m/sec) of W-waves in the transmitting and receiving trees. Ambiguity is present due to the time it took to make three

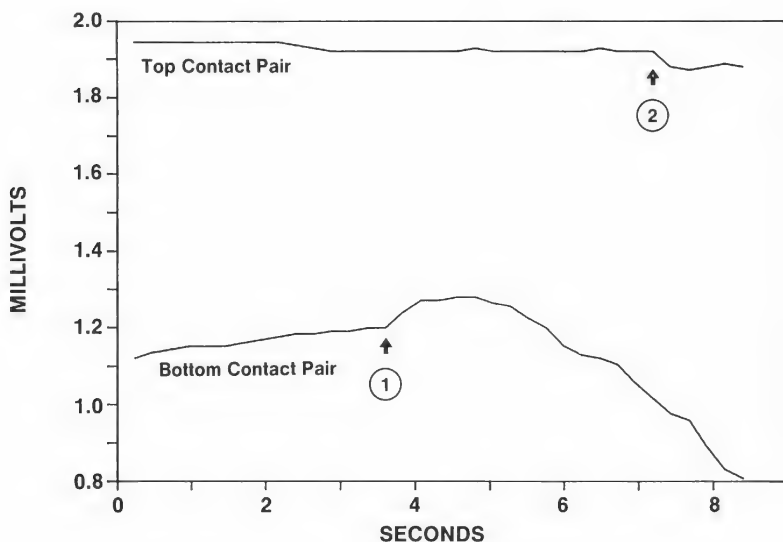


Figure 5. Results from a nail pushed quickly into the base of a salt solution filled tree section (Douglas fir (*Pseudotsuga menziesii*)). This sample was 7.5 cm in diameter at the base. A pair of probes spaced at 2.5 cm were placed along the sample at 30 cm from the base. Another pair of probes (spaced at 2.5 cm) were placed along the section at 3.75 cm from the top. The distance between the centers of the pairs of probes was 263.75 cm which when divided by 3.5 sec (the time between signal arrivals) gives about 75 cm/sec for the velocity in this case. (1) is the beginning of the response from the bottom contact pair and (2) is the beginning of the response from the top contact pair.

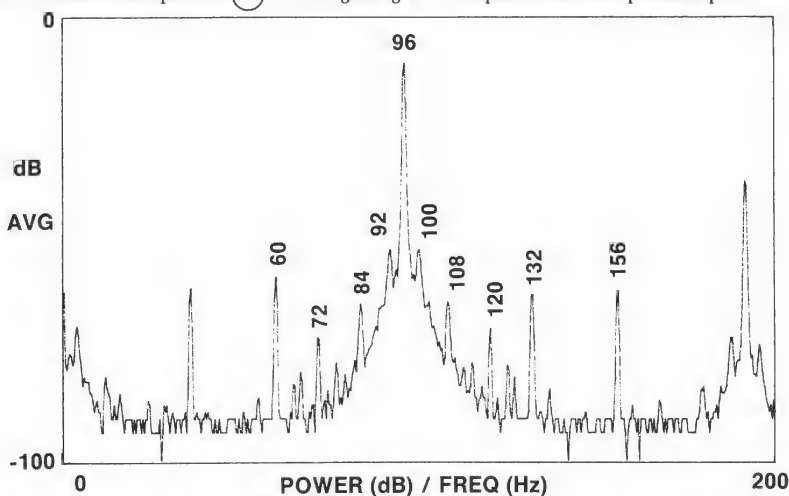


Figure 6. A sum and difference frequency spectrum (see the text) resulting from applying a small ac signal (96 Hz) along the stalk of a begonia plant (*Begonia* sp). The current source electrodes were 45 cm apart with 65 mv applied through a 50,000 ohm resistor. The electrodes with leads going to the spectrum analyzer were 3.5 cm apart along the stalk between the source electrodes. The first two peaks that are symmetrical about the 96 Hz peak were at 92 Hz and 100 Hz or at ± 4 Hz away from the 96 Hz peak. The next easily readable peaks are at ± 12 , ± 16.8 , ± 19.2 , ± 21.6 , ± 24 , ± 28.8 , ± 30.8 , ± 36 , ± 40.8 , and ± 60 Hz and so on away from the 96 Hz peak. Three of the frequencies represented here (19.2, 24, and 28.8 Hz) are integral multiples (harmonics) of 1.6 Hz while the others appear to be harmonics of a subharmonic of 1.6 Hz which here is 0.16 Hz (except for 30.8 Hz where it is 0.08 Hz). To the far right one sees the second harmonic of 96 Hz or 192 Hz.

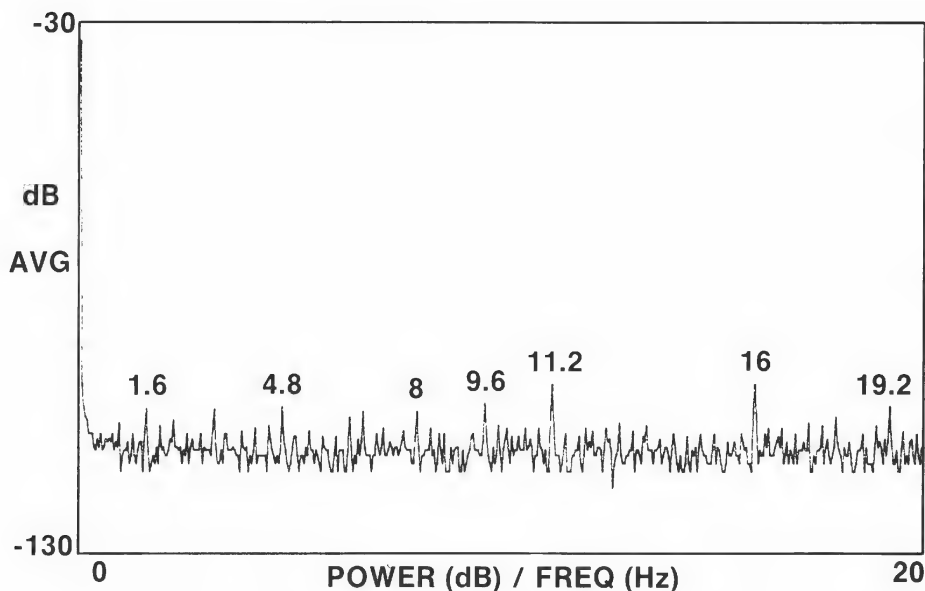


Figure 7. A spectrum from probes in a salt solution filled tree section (hazelnut, *Corylus* sp.) in an aluminum box. The spectrum is typical of spectra obtained from plants and solution filled tree sections outside the box. The 0.32 spaced peaks (for a 20 Hz baseband) are still present with the generally larger amplitude 1.6 Hz harmonics some of which are labelled.

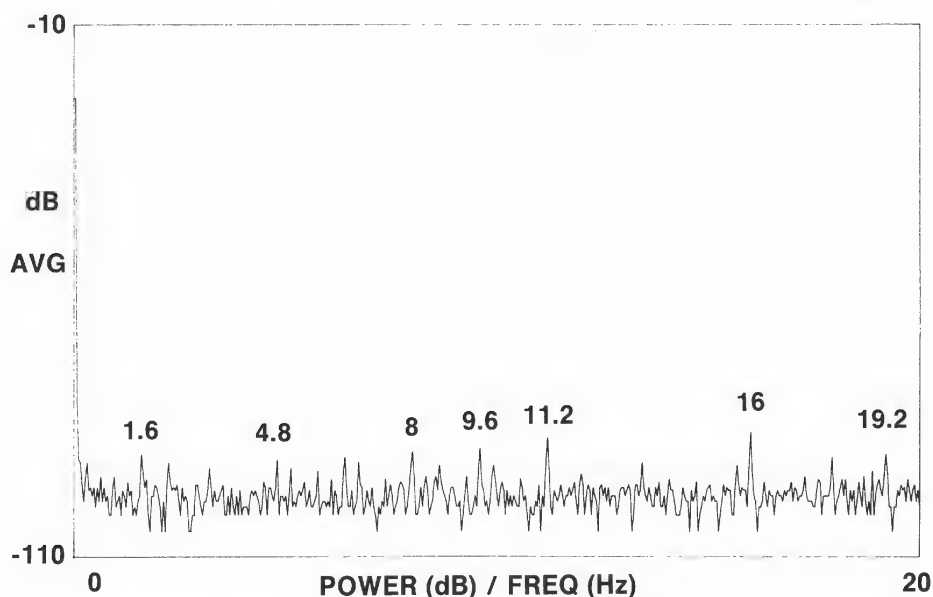


Figure 8. A spectrum taken from probes on a potted lemon (*Citrus Limon* sp.) tree 100 m underground in a mine shaft. The spectrum is similar to that obtained above ground from other plants and salt solution filled tree sections. It appears so far that W-wave phenomena are unaffected by shielding.

chops (less than 5 seconds). The received response (lower curve at about 20 seconds) is considerably smaller than the transmitting tree response but it is still quite appreciable when it is considered that W-wave effects are basically hard to detect due to the lack of good sensors and a lack of complete knowledge of the wave characteristics of a particular tree. The rises resulting from the reception of chop information usually had amplitudes of from 0.1 mv to 0.8 mv. The rise in the receiving tree curve preceding the received signal is a normal positive drift which often occurs on initial placement of probes. The top curve is the damage curve of Wagner 1988b. We see no apparent reflection blip because the results of several chops often obscure later curve structure but there are some roughness in the region where the reflection blip would be expected.

A processing time is likely required by receiving and transmitting trees. We attempted to reduce this effect by testing pairs of trees with presumably similar processing times to obtain velocities for signals traveling between trees. Of course, this may or may not be true because processing times may depend on signal strength, tree structure differences, etc. However, generally we obtained a velocity for signal travel between trees which was between 4.6 m/sec and 5.0 m/sec as the air (or ground) velocity (Table 1). The magnitude of the velocity would seemingly exclude tree root connections since the velocity in roots would probably be similar to that in the body of the plant. The between tree speed measured here is approximately five times the *in situ* velocity (96 cm/sec) (Wagner 1989h). The radical difference between the *in situ* velocity and this velocity suggests that

an air velocity was measured rather than a velocity through earth since salt filled sample tests give an even lower velocity for more dense materials. For example we found velocities of near 70 cm/sec by pushing in a nail at the base of fresh salt solution filled tree sections using time of flight measurement techniques (Figure 5). The velocity for W-waves obtained from Figure 5 is 75 cm/sec but an earlier test on the same sample (24 hours earlier) gave a velocity of 66 cm/sec and when the sample was pulled from solution the apparent velocity was 62 cm/sec. The loss of salt and water as the sample dried appeared to increase the W-wave velocity.

Conclusions and Observations

The data here suggest that plants communicate in a much more fundamental way than just by means of aerosols (Rhoades 1985). The data also suggest that this communication involves W-waves.

Still there is the challenge of developing a better transducer for these waves. These waves don't interact with anything very much and thus a really superior sensor might be difficult to construct. Trees and other plants with salt solution filled samples and capacitors seem to provide the best detectors so far.

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LETTERS TO THE EDITOR

On Impacts, Volcanoes, and Extinctions

Editor,—The theories on late Cretaceous and other mass extinctions are fascinating. Critical reviews include the one by Drake and Herman (1988) in *Northwest Science*; it was followed by an interesting letter to the editor in which Hooper (1988) related Deccan volcanism to Cretaceous-Tertiary boundary extinctions. The two main groups of theories regarding these extinctions are based on extraterrestrial (impact) events or enormous volcanic eruptions.

L. W. Alvarez and others (1980) proposed and championed the theory that the extinction of dinosaurs and many other species was triggered when a large bolide (asteroid, meteorite, or comet) collided with the earth 66 million years ago. The extinctions would have taken place in a very brief time span as an impact-generated dust cloud reduced photosynthesis long enough for plants to die (followed by herbivores and then carnivores). The chief objections to this theory are summarized by Officer and Grieve (1986): dinosaurs became extinct over several million years, terrestrial floral changes were selective, and ocean plankton changes occurred over 10,000 to 100,000 years. In other words, extinctions took place over too long a period of time to be explained by a single asteroid. As Patrick Spencer put it, "A meteorite may have happened to hit the last dinosaur, but the beasts were on the decline for millions of years before then" (pers. comm. 1988).

Officer and Drake (1983, 1985) have been the chief proponents of a theory that intense eruptive volcanic events caused the late Cretaceous extinctions. W. Alvarez (1986) rejected the volcanic eruption theory because a basaltic eruption would not produce shocked quartz and a silicic eruption would not result in iridium or silicic spherules. But what if a volcanic region produced both basaltic and silicic magmas? Consider examples from the Pacific Northwest alone. Mount St. Helens has erupted both quiet basalt flows and abundant dacitic pyroclastics in the last 2500 years (Mullineaux and Crandell 1981). In latest

Cenozoic there has been abundant basaltic and silicic volcanism on a much larger scale in the Yellowstone-eastern Snake River Plain region near the Wyoming-Idaho border. But we still have the problem of shocked quartz: "there are no occurrences of shocked quartz at unquestionable volcanic explosion sites" (Alvarez 1986, p. 653).

Another problem with volcanism is that even silicic explosions would produce only local tsunami. Bourgeois and others (1988) proposed that a sandstone bed at the Cretaceous-Tertiary boundary in Texas may be a tsunami deposit. They conclude that a huge tsunami may have been produced by a bolide impact within 5000 km of central Texas.

These theories are summarized in Table 1, which is modified from the report by Alvarez (1986). I have added two columns to his table: one for a combination of basaltic and silicic volcanism, the other for volcanic activity (basaltic and/or silicic) triggered by the impact of an extraterrestrial object. There are also two additional rows: one for tsunami deposits(?) and another for the time period over which the extinctions occurred.

The objections to the conflicting impact and volcanic theories for extinctions at the Cretaceous-Tertiary boundary may disappear if the mechanisms are combined. Our solar system has many examples of igneous activity believed to have been caused by impact. Dietz (1964) interpreted the Sudbury, Ontario, structure as a 1.7 billion-year-old asteroid impact that melted the country rock. "Because of its great magnitude, the Sudbury event triggered magmatism by offloading the lower crust and mantle and by adding shock heat. Partial fusion of already critically warm rock resulted. A saucer-shaped pool of magma—formed and differentiated in the crater bottom, also laying down a thick capping of welded tuffs—" (Dietz 1964, p. 412). Dietz also considered lunar maria to be created by impact-triggered magmatism. According to Murray and

TABLE 1. Comparison of impact and volcanic theories for late Cretaceous extinctions (based in large part on Alvarez, 1986).

Evidence	Impact(s) or other extraterrestrial event(s)	Volcanism: quiet basaltic	Volcanism: violent silicic	Volcanism: basaltic plus silicic	Impact plus volcanism
Iridium	Yes (Ir in meteorites)	Yes? (Ir in Kilauea gas)	No (Ir not yet found)	Yes?	Yes
Spherules (microtectites, etc.)	Yes (droplets of impact melt)	Yes (droplets of liquid basalt)	No (explosions produce angular fragments)	Yes	Yes
Shocked quartz	Yes (common at known im- pact sites)	No (explosions uncommon)	No? (probably insufficient shock in explosions)	No?	Yes
Soot?	Yes? (wildfires might be extensive)	No? (wildfires probably only local)	No? (wildfires probably only local)	No?	Yes?
Tsunami deposits?	Yes (if in or near ocean)	No (explosions uncommon)	Yes? (tsunami effects local)	Yes?	Yes
Worldwide distribution	Yes (if bolide large enough)	No? (eruption not violent enough)	Yes? (if eruption violent enough)	Yes?	Yes
Instant extinction	Yes? (days to years)	No? (if eruptions lasted thousands to millions of years, extinctions might take that long)	No?	No?	Not necessarily
SUMMARY	REJECTED if extinctions not instant	REJECTED on basis of shocked quartz	REJECTED on basis of Ir and spherules	DOUBTFUL on basis of shocked quartz	ACCEPTABLE

others (1981, p. 21), partial filling of some lunar basins "by impact melt was followed by sporadic emplacement of mare basalts from both flood-type [basalt plateau] and plains-type [coalescing shields, cones, and fissure flows] eruptions."

Demonstration that both impact and volcanism occurred at the end of the Cretaceous would explain worldwide distribution of iridium, spherules, shocked quartz, soot(?), and tsunami deposits(?). Furthermore, intense volcanism lasting thousands to millions of years could explain the gradual disappearance of dinosaurs and other life. Hooper (1988) reports that all Deccan

volcanism in India occurred in perhaps less than one million years at about 67 million years ago. That volcanism was probably produced by a hot spot in the mantle now under Reunion Island in the Indian Ocean. What turned on the volcanism of the Deccan Plateau? Was it an impact? Have tsunami deposits been reported at the K/T boundary in Eurasia or Africa?

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Northwest Science

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Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Avoid unnecessary tables. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues. The manuscript should consist of sections in the following sequence: title page, abstract, main text, literature cited, footnotes, tables, figure legends.

The title page is the first page of the manuscript and includes all the following: author's name (or names), institutional address from which the manuscript emanated, title of the paper, running head, total number of supplements (figures, graphs, and tables), and conclude with the full address and telephone number of the one individual to whom galley proofs should be sent.

The purpose of an abstract is to summarize briefly the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the main text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study, indicating why the study was undertaken. Next the experimental design or approach should be stated and the results summarized. Finally, the abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a 1/3 to 1/2 reduction in size, but not overly large.

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HANFORD WILDLIFE
Past and Future

NORTHWEST SCIENCE



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Announcements

In This Issue

In 1943, mostly undeveloped land along with its wildlife in southeast Washington was acquired by the federal government to become a site for production of nuclear materials. This was the Hanford Site eventually to come under the jurisdiction of the U.S. Department of Energy. The fate of the wildlife on the Hanford Site and its future are the subject of the featured article by William Rickard and Linda Poole.

From the Annual Meeting

The annual meeting of the Northwest Scientific Association was held in Richland, Washington and was hosted by the Tri-Cities University Center. In addition to symposia and contributed papers, research grants were announced.

Research Grants

Research grants were awarded to each of the following students:

Laura Morrison, Oregon State University
Markolf Teiser, University of Oregon
Sanjayan Mutlingham, University of Oregon
Shawn Cummings, Washington State University
Albert G. Wilson, Jr., Washington State University
Rex Sallabanks, University of Oregon

These grants will be awarded again in 1990. More details on nomination and application procedures will appear in the November issue of *Northwest Science*.

Upcoming Annual Meeting of the Northwest Scientific Association

The 1990 meeting of the Northwest Scientific Association will be held at Oregon State University, Corvallis. More details in the November issue.

ANNOUNCEMENT OF INTEREST

Rare Lichens Project: A project to determine the conservation status of the lichens of North America north of Mexico, and Hawaii was recently begun by Mason E. Hale, Jr., and Sherry K. Pittam of the Department of Botany, Smithsonian Institution, in cooperation with The Nature Conservancy.

The project's goal is to generate a list of rare or endangered lichens with the necessary information to seek protection for species as appropriate, and to provide this information to the Conservancy and to other conservation organizations and land-management agencies. When possible, potential threats to individual species, as well as geographic distribution and abundance, will be noted. Taxonomy will follow Egan's checklist (as revised).

Those interested are invited to provide names of potentially rare or endangered species of lichens, with available supporting information. Please send to Sherry K. Pittam, Rare Lichens Project, Smithsonian, Botany/NHB 166, Washington, D.C. 20560. Telephone: (202) 357-2545.

Life History, Ecology and Population Status of Migratory Bull Trout (*Salvelinus confluentus*) in the Flathead Lake and River System, Montana

Abstract

Life history, ecology, and population trends of migratory bull trout (*Salvelinus confluentus*) were investigated in the Flathead Lake and River system of northwest Montana and southeast British Columbia. We conducted these studies to obtain information to manage the species in light of threats posed by timber harvest, hydropower development, and a proposed coal mine. We estimated that about half the adult bull trout in Flathead Lake embarked on a spawning migration from May through July, swimming 88-250 km to reach tributaries of the North and Middle Forks of the Flathead River. Bull trout entered the tributaries when water temperatures dropped below 12°C, and spawned from late August through early October after water temperatures were below 9°C. They spawned in areas of tributaries with low gradient, loosely compacted gravel, groundwater influence, and cover. After spawning, females left the tributaries and returned to the lake sooner than males. Most spawners were six or seven years old and they averaged 628 mm in length. Juveniles were found close to the substrate in streams with summer maximum temperatures less than 15°C. Juveniles migrated out of the tributaries to the river system from June through August, at age I (18%), II (49%), III (32%), and IV (1%). Population status was monitored through redd counts and estimates of juvenile abundance in natal tributaries. The population may be limited by quantity and quality of rearing and spawning habitat, and spawning escapement. Specific requirements for spawning and rearing habitat, and general sensitivity of each life stage, make the bull trout an excellent indicator of environmental disturbance.

Introduction

The bull trout (*Salvelinus confluentus*) is the largest species of fish native to the Flathead drainage, attaining a length of nearly one meter and a weight of 10 kg. The bull trout inhabiting the inland waters of northwestern North America is considered a separate species from the smaller, coastal Dolly Varden (*Salvelinus malma*) (Cavender 1978). The bull trout population in the Flathead system is largely migratory, growing to maturity in lakes and migrating through the river system and into the tributaries to spawn. Juveniles live in tributary streams from one to four years before migrating to the lakes.

Much information has been published concerning the life history of coastal Dolly Varden (e.g., Blackett 1968, Armstrong and Morton 1969, Armstrong and Morrow 1980, Balon 1980). Published information on the bull trout is limited. McPhail and Murray (1979), Leggett (1969), and Allan (1980) studied various aspects of the life history of bull trout in British Columbia and Alberta. Gould (1987) described the characteristics of larval bull trout.

The Montana Department of Fish, Wildlife and Parks has studied the bull trout population in the Flathead drainage since 1953 (Block 1955, Hanzel 1976). More intensive work was undertaken from 1979-1984 during the EPA-sponsored

Flathead River Basin Studies (Graham *et al.* 1980, Fraley *et al.* 1981, Shepard *et al.* 1982, 1984b, Graham *et al.* 1982, Fraley and Graham 1982, Graham and Fredenberg 1982, Leathe and Graham 1982). We studied bull trout age and growth both in the lake and in the river system, harvest by anglers, the adult spawning migration, spawning site selection and use, and the densities, habitat selection, and emigration of juveniles growing in tributaries. Methods included tagging, gillnetting, stream trapping and electrofishing, creel survey, otolith and scale analysis, redd counts, and substrate analysis (Graham and Fredenberg 1982, Shepard and Graham 1983).

In this paper we summarize our findings on the life history, ecology, and population status of adfluvial bull trout in the Flathead Lake and inlet river system and compare our information to the results of other investigators.

Study Area

The Flathead Lake and River system is a headwater drainage of the Columbia River Basin (Figure 1). Flathead Lake is a large oligomesotrophic lake with a surface area of 476 km² and a mean depth of 32.5 m (Potter 1978). The upper 3 m of Flathead Lake is regulated by Kerr Dam, constructed on the outlet in 1938. The Flathead River enters the north end of the lake. This study

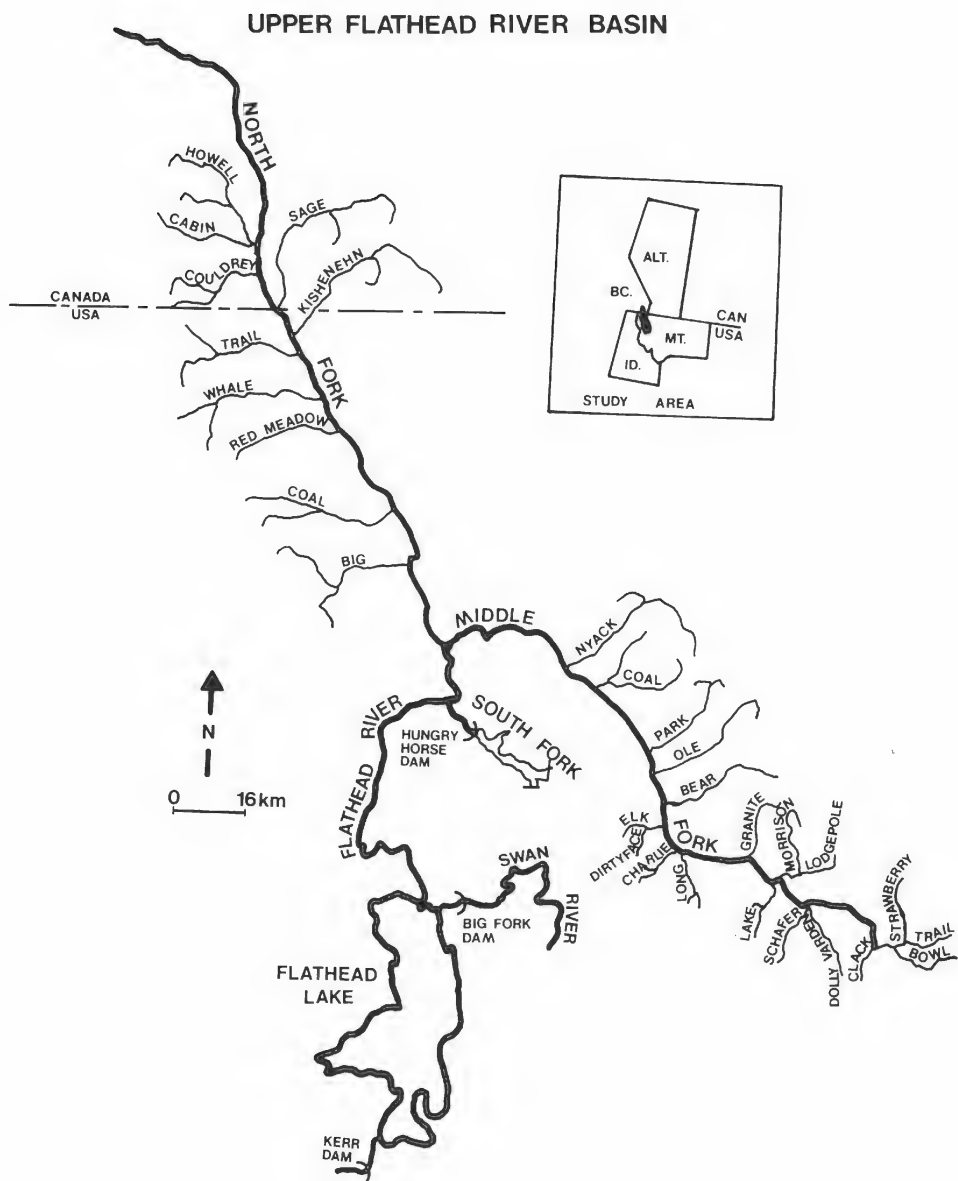


Figure 1. The upper Flathead River Basin. The 28 tributaries shown were used by spawning bull trout.

was conducted in the upper Flathead Basin which includes Flathead Lake and the river system upstream from Flathead Lake.

The South, Middle and North forks drain areas of approximately equal size in portions of the Great Bear and Bob Marshall wildernesses, Glacier National Park and the Flathead National Forest. The upper North Fork drains southern British Columbia. The South Fork is regulated by Hungry Horse Dam, located 8 km above its mouth. The Swan River enters Flathead Lake near the mouth of the Flathead River. Bull trout coexist with 23 other species of fish in the Flathead Lake and River system (Leathe and Graham 1982).

Most bull trout that spawn in the North and Middle Fork drainages mature in Flathead Lake, but fish maturing in large lakes of Glacier National Park may spawn in some tributaries. There are a few populations of bull trout in tributaries of the North Fork that spend their entire lives in the streams.

Bull trout originally used the tributaries of all forks of the Flathead and the Swan rivers. The construction of Bigfork Dam in 1902 blocked bull trout migrations into the Swan River. Limited numbers of bull trout move downstream from the Swan drainage via a marginal fish ladder, as evidenced by tag returns. Hungry Horse Dam, a 164.6-m structure which was closed in 1951, blocked all movements of bull trout into the South Fork drainage and probably resulted in a substantial reduction of the population in Flathead Lake.

The 28 tributaries used by spawning bull trout in the North and Middle Fork drainages (Figure 1) are characterized by gravel-rubble substrate, low flows of 0.057-1.70 m³/sec, and maximum summer water temperatures less than 15°C.

Results and Discussion

Life History

Lake Residence

Bull trout populations residing in Flathead Lake were found to include recently arrived juveniles from the Flathead River system, subadult fish less than about 450 mm in length, and mature fish five to six years or more in age. Most bull trout in Flathead Lake matured at age VI. A similar

age of maturity was reported for bull trout in Arrow Lakes, British Columbia (McPhail and Murray 1979).

The diet of bull trout in the lake consisted almost exclusively of fish. Whitefish species and yellow perch (*Perca flavescens*) were the most important food items, followed by kokanee (*Oncorhynchus nerka*) and nongame species (Table 1). Small bull trout have been found to feed incidentally on *Mysis* in Flathead Lake. *Mysis relicta* was discovered in Flathead Lake in 1981 and densities increased dramatically through 1986. Kokanee were the major food item for bull trout in Pend Oreille Lake, Idaho (Jeppson and Platts 1959), while whitefish were the major food in Upper Priest Lake (Bjornn 1961).

The annual growth increment for bull trout in Flathead Lake, based on analysis of scales, ranged from 60-132 mm (Table 2). Back calculations of length at annulus formation were made from 1,813 scale samples. Aging was checked with otoliths from 451 of the fish. Agreement of aging between otoliths and scales ranged from 100 percent for fish zero to three years of age, to 52 percent for older, mature fish. Growth of lake-resident fish was relatively constant after age IV. Growth rates of bull trout in Flathead Lake were similar to those reported for Priest and Upper Priest Lakes, Idaho (Bjornn 1961).

Not all mature bull trout spawned annually. Adult-size fish were relatively less abundant in the lake during the summer and fall, as compared to the spring. It appeared that 38 to 69 percent (average 57%) left the lake each spring and summer to spawn. The frequency of successive year spawning varied by age and sex (Leathe and Graham 1982). Alternate year spawning has been reported for inland Dolly Varden char (Armstrong and Morrow 1980).

Upstream Migration

Bull trout maturing in Flathead Lake began their spawning migration into the river system during April and moved slowly upstream, arriving in the North and Middle forks during late June and July. They traveled more than 250 km to spawn in some North Fork tributaries in British Columbia. The shortest distance traveled from Flathead Lake was 88 km to the mouth of Canyon Creek in the North Fork drainage. Observations and tag returns from 1974-1982 indicated that adult bull

TABLE 1. Composition by number, weight, and frequency of occurrence and calculated index of relative importance (IRI, George and Hadley 1979) for major food items in the stomachs of 95 bull trout collected between November and January, 1979, 1980 and 1981 in Flathead Lake.

Item	Number	(%)	Wet weight -g.	(%)	Index of Relative Importance (IRI)
Pygmy whitefish	5	(2.4)	37.0	(4.0)	3.2
Lake whitefish	1	(0.5)	104.1	(11.2)	4.3
Mountain whitefish	1	(0.5)	24.3	(2.6)	4.4
Unidentified whitefish	11	(5.3)	281.2	(30.3)	15.0
Total whitefish	18	(8.7)	446.6	(48.1)	23.5
Kokanee	2	(1.0)	82.8	(8.9)	4.0
Unidentified trout/salmon	2	(1.0)	13.2	(1.4)	1.5
Total trout/salmon	4	(1.9)	96.0	(10.3)	5.1
Sculpin	3	(1.5)	7.6	(0.8)	1.8
Redside shiner	5	(2.4)	15.0	(1.6)	2.0
Peamouth	1	(0.5)	3.6	(0.4)	0.7
Sucker	2	(1.0)	74.4	(8.0)	3.7
Yellow perch	83	(40.3)	105.1	(11.3)	24.6
Total nongame	94	(45.6)	205.7	(22.1)	31.0
Unidentified fish	90	(43.7)	181.1	(19.5)	41.4

TABLE 2. Back calculated lengths at annulus formation of bull trout in the upper Flathead Basin (n in parentheses). Calculations were made based on methods in Hesse (1977).

Drainage	Total length (mm) at annulus								
	I	II	III	IV	V	VI	VII	VIII	IX
<i>Adults and Juveniles</i>									
Upper Flathead (1968-81)	66 (1,813)	121 (1,538)	196 (1,161)	292 (927)	385 (669)	475 (349)	566 (129)	657 (32)	731 (4)
Flathead Lake (1968-81)	68 (931)	129 (931)	204 (928)	291 (853)	384 (603)	472 (291)	566 (102)	658 (28)	731 (4)
North Fork of the Flathead River drainage (1975-81)	73 (533)	117 (306)	165 (60)	301 (12)	440 (8)	538 (7)	574 (3)	—	—
Middle Fork of the Flathead River drainage (1980-81)	52 (349)	100 (300)	165 (172)	297 (61)	399 (57)	488 (50)	567 (24)	655 (4)	—
<i>Juveniles Only</i>									
North Fork drainage	73 (525)	117 (298)	155 (52)	228 (4)	—	—	—	—	—
Coal Creek	75 (145)	124 (62)	202 (23)	323 (14)	—	—	—	—	—
Red Meadow Creek	65 (145)	113 (113)	168 (29)	360 (7)	—	—	—	—	—
Trail Creek	74 (473)	119 (264)	158 (46)	228 (4)	—	—	—	—	—
Whale Creek	56 (52)	98 (34)	139 (6)	—	—	—	—	—	—

trout remained at the mouths of spawning tributaries for two to four weeks during which time feeding was thought to be limited.

Based on observations at stream trapping sites, adult bull trout entered tributary streams at night from July through September; the majority entered in August. Because most bull trout moved through the traps in pairs, we believe bull trout formed pairs near the mouth of the spawning tributary. Bull trout which entered the spawning tributaries were generally not in final spawning condition, but held in the tributaries for up to a month or more in deeper holes or near log or debris cover before spawning. Similar pre-spawning behavior and spawning timing was reported for bull trout in Mackenzie Creek (McPhail and Murray 1979) and John Creek (Leggett 1969) in British Columbia.

Most bull trout spawners in the North and Middle Forks were six or seven years of age (Table 3) whereas most spawners in the Swan system were five or six years old (Leathe and Enk 1985).

TABLE 3. Age of bull trout spawners in the Flathead system.

Stream	Percent by Age				
	5	6	7	8	9
North Fork Flathead River 1954 (N = 41)	24	39	34	3	0
Middle Fork Flathead River 1981 (N = 31)	10	48	35	10	0
Swan River 1983 (N = 57)	33	35	23	9	<1
Swan River 1984 (N = 76)	43	37	17	3	0

Spawning

Most bull trout spawned during September and early October in the Flathead River system, as did adfluvial bull trout in Idaho (Heimer 1965) and British Columbia (McPhail and Murray 1979). Initiation of spawning in the Flathead appeared to be related largely to water temperature, although photoperiod and streamflow probably also played a part. Spawning began when water temperatures dropped below 9-10°C. McPhail and Murray (1979) reported that 9°C was the threshold temperature for the initiation of spawning in Mackenzie Creek, British Columbia.

Bull trout spawners selected areas in the stream channel characterized by gravel substrates, low compaction and low gradient (Table 4). Groundwater influence and proximity to cover also were important factors influencing spawning site selection. These relatively specific requirements resulted in a restricted distribution of spawning in the Flathead drainage. Bull trout from Flathead Lake spawned in only 28 percent of the 750 km of available stream habitat according to basin-wide surveys from 1980-1982.

TABLE 4. Mean measurements of physical habitat variables in 34 stream reaches where no redds were located, 29 reaches where redd frequency averaged 1.2 redds/km (low), and 31 reaches where redd frequency averaged 6.9 redds/km (high).

Parameter	Redd frequency categories		
	None	Low	High
Stream order	3.0	3.1	3.6
D-90 (cm; the size of material larger than 90% of the substrate)	51	37	33
Gradient (percent)	3.2	1.8	1.5
Boulder (percent of substrate)	16	12	10
Gravel-Cobble (combined percent of substrate)	54	62	62
High quality pool (percent of stream)	5	7	8
Overhang cover (percent)	14	10	11
Total cover (percent)	16	15	13

Average length of adult spawners in the Flathead River system was 628 mm (Table 5). The female chose a spawning site and constructed the redd, while the male defended the area. Male bull trout in Trail Creek, a North Fork tributary,

TABLE 5. Average total lengths of adult bull trout spawners in the Flathead drainage.

Stream	Year	Average Length (mm)	Number of Fish
North Fork	1979	638	36
	1977	645	32
	1953	617	165
Middle Fork	1980	618	35
	1957	622	87
Both Forks	1975	628	46

remained near the redd an average of two weeks after spawning. Bull trout redds in the Flathead drainage averaged 2.0 m long x 1.0 m wide, and sometimes overlapped. Block (1955) observed one male spawn with three females in succession; the size of the redd expanded each time. McPhail and Murray (1979), Leggett (1969), and Block (1955) provided detailed descriptions of spawning behavior and spawning site activities. After spawning, the spent adults moved out of the tributaries and downstream to the lake, possibly feeding on mountain whitefish (*Prosopium williamsoni*) during the journey.

Fecundity varied with fish size, averaging 5,482 eggs per female for a sample of 32 adults averaging 645 mm. One female bull trout weighed 15 pounds and contained 12,000 eggs. Bull trout in Arrow Lakes, British Columbia, were smaller and contained fewer than 2,000 eggs per female (McPhail and Murray 1979). The sex ratio of bull trout spawners averaged 1.4 females per male in Trail Creek in the North Fork drainage, and 1.37 females per male in the Swan drainage.

Incubation and Emergence

After deposition by early October, bull trout embryos incubated in the redd for several months before hatching in January. The alevins then remained in the gravel and absorbed the yolk sac, with the first fry appearing in electrofishing samples in mid April. Emergence occurred approximately 200 days after egg deposition. Newly emerged fry averaged 23-28 mm and more than doubled their length during the first summer of growth (see Table 2).

Weaver and White (1985) found that incubation time was dependent on temperature. Bull trout eggs required 113 days (340 temperature units) to 50 percent hatch in Coal Creek, a tributary of the North Fork of the Flathead River. The fry emerged from the gravel 223 days (635 temperature units) after egg deposition. Intergravel temperatures during the incubation period (October-March) in Coal Creek ranged from 1.2-5.4°C. Survival to emergence in Coal Creek averaged 53 percent. McPhail and Murray (1979) reported the best survival of bull trout embryos at 2-4°C.

Juvenile Occurrence and Emigration

Juvenile bull trout were present in about half of the stream reaches surveyed during studies in the

upper Flathead River Basin. Juveniles were present in many reaches that were not used by adult spawners; they apparently swam upstream to these sections to grow. Distribution also was influenced by water temperature as juvenile bull trout were rarely observed in streams with summer maximum temperatures exceeding 15°C. Oliver (1979), Allan (1980) and Pratt (1984) also reported that bull trout distribution was affected by temperature.

Young-of-the-year bull trout were generally found in side channel areas and along the stream margins in Flathead tributaries. Blackett (1968) reported a similar habitat preference for juvenile Dolly Varden char in southeast Alaskan streams. McPhail and Murray (1979) found young-of-the-year bull trout in areas of low velocity near stream edges.

Densities of bull trout juveniles in Flathead tributaries were greatest in pools, and lower but generally similar in runs, riffles and pocketwater habitat. Juvenile bull trout were found closely associated with stream substrate. Pratt (1984) studied microhabitat preferences in the Flathead drainage and reported that juvenile bull trout (less than 100 mm) usually remained near the stream bottom, close to streambed materials and submerged fine debris. Juveniles 100 mm or longer also remained near cover, including larger instream debris. As the juvenile bull trout grew, they became less associated with the streambed.

During stream residence, juvenile bull trout were opportunistic feeders, mainly ingesting aquatic invertebrates (especially Diptera and Ephemeroptera) in similar percentages as they were available in the stream (Fraley *et al.* 1981). Bull trout larger than 110 mm also ate small trout and sculpin.

Snorkeling estimates of juvenile bull trout densities in Flathead drainage tributaries averaged 1.5 fish/100 m² of stream surface area (range: 0.1-7.1). Juvenile bull trout are difficult to observe because of their close association with the stream bottom, so these numbers are probably underestimates. Electrofishing estimates ranged as high as 15.5 fish/100 m² in certain streams.

Most juvenile bull trout in the Flathead drainage remained in the tributaries for one to three years before emigrating to the river system. Of 246 juvenile bull trout captured in downstream

migrant traps placed in three tributaries to the North and Middle forks, about half (49%) were age II, a third (32%) age III, and 18 percent age I (Table 6). Only 1 percent of the emigrants were age IV. The ages of emigrating juveniles were similar in Idaho and British Columbia (Bjornn 1961, Oliver 1979, McPhail and Murray 1979). The average lengths at annulus formation of Age I, II, and III juvenile bull trout in tributaries of the North Fork Flathead were 73, 117 and 155 mm, respectively (Table 2).

TABLE 6. Percent and number of age I, II, III and IV bull trout emigrating from tributary streams.

Location	Years of migration sampling	Age Classes			
		I	II	III	IV
Red Meadow Cr.	1973, 79	6 (3)	76 (42)	18 (10)	0 (0)
Trail Creek	1977, 79	34 (41)	43 (52)	19 (23)	3 (4)
Geifer Creek	1981	0 (0)	37 (26)	63 (45)	0 (0)
All Sites	(%) (number)	18 (44)	49 (120)	32 (78)	1 (4)

Emigration of juveniles from the tributaries into the Flathead River system took place largely from June through August (Table 7), similar to the emigration period reported for the Wigwam drainage, British Columbia (Oliver 1979). After juvenile bull trout entered the river system they appeared to move rapidly downstream into the main stem Flathead River, arriving below the South Fork during August and September. Although juvenile bull trout were captured by electrofishing in the main stem throughout the year, their numbers peaked during the fall months (McMullin and Graham 1981). Snorkel observations indicated that some juveniles lived along the shallow margins of the Middle and North forks. Residence in the lower Flathead River before entry into Flathead Lake has not been well documented.

Trends in Spawner Abundance

Drainage-wide counts of bull trout redds in 1980 (568), 1981 (714), 1982 (1138), and 1986 (814) were used to index the number of adfluvial bull trout

which successfully spawned in the river-tributary system. We converted the redd counts to approximate fish numbers by making the following assumptions: 1) 75 percent of all redds were located, and 2) an average of 3.2 spawners entered the tributary for each completed redd. From partial trapping results on several tributaries in 1977-1981, we estimated a spawner:red ratio of 3.2:1. In 1953, 55 bull trout entered Trail Creek and constructed 18 redds for a spawner:red ratio of 3.2:1 (Block 1955). During 1954, 160 bull trout constructed 48 redds in Trail Creek, yielding a ratio of 3.3:1. Based on these assumptions, we calculated that an average of 3,450 bull trout successfully spawned annually in the Flathead drainage during our period of record.

Bull trout spawned in 28 tributaries to the North and Middle forks (see Figure 1), but only a small percentage of the stream reaches were used for spawning. Important spawning tributaries in the North Fork were Howell, Trail, Whale, Big and Coal creeks. Major spawning tributaries in the Middle Fork were Morrison-Lodgepole, Granite, Ole, Trail and Dolly Varden creeks. The portion of the drainage in Canada supported 23-31 percent (mean 29%) of the spawning in the North Fork drainage during the 1980-82 period. Howell Creek supported 13-19 percent (mean 16%) of all North Fork spawning.

Monitoring of bull trout spawning at selected sites indicated that escapement was highest in 1982 (Table 8). These sites are considered representative of the drainage, and comprised 32, 30, 31, and 43 percent of the total drainage-wide counts in 1980, 1981, 1982, and 1986, respectively. Monitoring areas reflected drainage-wide trends.

Juvenile bull trout densities have been used as an index of population status. Juvenile bull trout populations in sections of Coal and Morrison creeks have been monitored for a six-year period (Table 9). Numbers of juvenile bull trout in these sections were highest in 1987 for both streams. Continued population estimates in these streams will provide valuable baseline information for future monitoring.

Sampling for bull trout in Flathead Lake indicated that the population had been relatively stable through 1981. Average catches of bull trout in sinking nets were 1.2 to 2.1 fish per net

TABLE 7. Number of stream trapping days, number of juvenile bull trout passed downstream through traps, and number of trapped juvenile bull trout per trap day by month from North Fork tributaries during 1976 to 1980 and Middle Fork tributaries during 1981.

	June	July	August	September	October
<i>North Fork tributaries (1976-1980)</i>					
Trap days	42	443	424	264	131
Number of fish	42	709	340	116	6
Fish/trap day	1.00	1.60	0.80	0.44	0.04
<i>Middle Fork tributaries (1981)</i>					
Trap days	43	74	62	14	—
Number of fish	60	28	19	8	—
Fish/trap day	1.40	0.38	0.26	0.57	—

TABLE 8. Bull trout redd counts for selected areas of tributaries chosen for monitoring in the Flathead Drainage.

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
<i>North Fork:</i>										
Big	10	20	18	41	22	9	9	12	22	19
Coal	38	34	23	60	73	61	40	13	48	52
Whale	35	45	98	211	141	133	94	90	143	136
Trail	34 ^a	31 ^a	78	94	56	32	25	69	64	62
Total North Fork	117	130	217	406	292	235	168 ^b	184	277	269
<i>Middle Fork:</i>										
Morrison	25 ^a	75	32 ^a	86	67	38	99	52	49	50
Granite	14	34	14 ^a	34	31	47	24	37	34	32
Lodgepole	32	14	18	23	23	23	20	42	21	19
Ole		19	19	51	35	26	30	36	45	59
Total Middle Fork	71	142	83	194	156	134	173 ^b	167	149	160
Total Drainage Monitoring Areas	188	272	300	600	448	369	341	351	426	429

^aCounts may be underestimated due to incomplete survey.

^bHigh flows may have obliterated some of the redds.

TABLE 9. Juvenile bull trout densities in sections of a North Fork tributary (Coal Creek) and a Middle Fork tributary (Morrison Creek) from 1980-1985.

	Date	Population Estimate (Number/150 m section)	95% Confidence Interval
Coal Creek (at Deadhorse Bridge)	08/05/82	130	± 36
	03/23/83	99	± 33
	08/31/84	89	± 27
	08/26/85	167	± 66
	08/12/86	149	± 45
	09/01/87	179	± 55
Morrison Creek	09/23/80	91	± 48
	09/01/82	93	± 5
	08/18/83	62	± 11
	09/25/85	93	± 27
	08/27/86	114	± 15
	08/25/87	138	± 10
	08/30/88	126	± 23

in 1967-1970, 2.2 to 2.9 fish per net in 1980-81 (Leathe and Graham 1982). Average length of bull trout sampled in Flathead Lake increased by 24 mm from 1967 to 1980. A larger percentage of the fish were greater than 500 mm in the 1980-81 sampling period. The percentage of trophy fish (greater than 634 mm) was similar in both sampling periods. Migrating spawners, captured in the river system, were similar in size from 1953 through 1981 (see Table 5).

Sensitivity to Environmental Disturbance

All bull trout life stages are sensitive to environmental disturbances. The population in the Flathead system is threatened by several major forms of resource development. The proposed Cabin Creek coal mine in the North Fork drainage in British Columbia received preliminary approval by the Canadian government and was referred by the U.S. and Canadian governments to an International Joint Commission for review (Flathead International Study Board 1988). This mining activity could harm bull trout spawning and rearing habitat in the upper North Fork and in Howell Creek, the major spawning tributary in the Canadian portion of the drainage. The major concerns are increased sedimentation, alteration of flow and water quality degradation (Biological Resources Committee 1987). In addition, timber harvest and road construction in both the North and Middle Fork drainages are potential threats to bull trout spawning and rearing habitat.

Increased fishing pressure is often associated with resource development. Because of the restricted distribution of bull trout spawning in the basin and the limited size of the known annual escapement (3,000-4,000 individuals), harvest of fish by anglers could reduce the population. Any increase in harvest by anglers in a particular area or subbasin could result in a loss of recruitment from that site, in turn reducing the overall population in Flathead Lake.

The long overwinter incubation and development phase for bull trout embryos and alevins (223 days in Coal Creek) leaves them particularly vulnerable to increases in fine sediments and degradation of water quality. In laboratory experiments, survival was shown to be inversely

related to the percent fine material (<6.35 mm) in the gravels (Weaver and White 1985). Survival to emergence ranged from nearly 50 percent in substrates which contained 10 percent fines, to zero percent in mixtures which contained 50 percent fines. Juvenile bull trout could be affected by streambed changes because of their close association with the substrate. Shepard *et al.* (1984a) found a significant relationship ($r^2 = 0.40$, $P < .01$) between substrate score (a measure of unimbedded instream rock cover) and juvenile bull trout densities in tributaries of the Swan River.

As our studies of bull trout in the Flathead River system continue, we hope to define more precisely the factors which negatively affect the population. It is not clear whether the tributaries are at carrying capacity for juvenile bull trout, nor whether juvenile densities are limited by spawner escapement levels. The answer to these questions will require monitoring of the escapement levels and resulting juvenile densities in the tributaries over a longer period of time. McPhail and Murray (1979) suggested that limitations in juvenile rearing habitat may form an "ecological bottleneck," greatly affecting overall population levels of bull trout.

Bull trout in the Flathead River system are dependent on habitat quality and management of the interconnected river, lake, and tributaries. Cumulative losses of spawning and rearing habitat would reduce the bull trout population in Flathead Lake.

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Response of Round-headed Buckwheat to Summer Burning

Abstract

Wildfires are common in the shrubsteppe region of the western United States, but there is little information concerning the response of shrubs that grow on rock outcrops to burning. We thus examined the response of an isolated stand of round-headed buckwheat to two August wildfires. The pre-burn stand density of round-headed buckwheat plants averaged 133 plants per 100 m². In the first growing season following a wildfire in August 1984, density was reduced to 47 plants per 100 m². In the second growing season after the initial burning, almost all of the surviving burn-damaged plants produced flowers. Following a second wildfire in August 1987, density was reduced to 7 plants per 100 m². Despite the fact that the buckwheat plants were widely spaced and past the flowering stage, and that the shallow, stony soil supported only a sparse stand of herbaceous plants with low fuel potential, round-headed buckwheat plants were vulnerable to late summer burning.

Introduction

Wildfires are a common occurrence in the shrubsteppe region of the western United States (Wright *et al.* 1979), as they are on the Hanford Site in southcentral Washington. Ignition is caused by lightning strikes, usually in late July or August when shrub, grass, and forb tissues are at seasonal dryness and air temperatures are near maximal (Stone *et al.* 1983). Most shrubsteppe shrubs are sensitive to summer wildfire. Sagebrush, *Artemisia tridentata*, bitterbrush, *Purshia tridentata*, and spiny hopsage, *Grayia spinosa*, are easily killed by summer burning (Uresk *et al.* 1976, Britton and Clark 1985, Rickard and McShane 1984). Rabbitbrush, *Chrysothamnus spp.*, has some capacity to sprout following summer burning (Daubenmire 1975, Bunting 1984); greasewood, *Sarcobatus vermiculatus*, unlike most other shrubs, sprouts readily after burning (Rickard and McShane 1984). As far as is known, there is no written documentation of the response of round-headed buckwheat, *Eriogonum sphaerocephalum*, to burning, but there is some information from Idaho that indicates that several species of *Eriogonum* other than *sphaerocephalum* are vulnerable to summer burning (Pechanec *et al.* 1954).

This paper documents the response of a single isolated stand of round-headed buckwheat to two August wildfires which burned in 1984 and again in 1987.

Location, Burn and Grazing History, and Methods

The buckwheat stand is located on the U.S. Department of Energy's Hanford Site in Benton

County, Washington, Section 9, Range 27E, Township 10N and is representative of the *Eriogonum sphaerocephalum*/*Poa sandbergii* association as described by Daubenmire (1970). The elevation of the stand is 180 m above mean sea level and precipitation averages 19.7 cm annually (Stone *et al.* 1983). The stand is confined to a basalt rock outcrop surrounded by deeper soil that supports stands representative of the *Artemisia tridentata*/*Poa sandbergii* association (Daubenmire 1970). The herb understory is sparse and dominated by Sandberg's bluegrass, *Poa sandbergii*, with only small quantities of cheatgrass, *Bromus tectorum*, bottlebrush squirrel tail, *Sitanion hystrix*, and Thurber's needlegrass, *Stipa thurberiana*. Neither the stand nor the surrounding area has been grazed by livestock for at least 40 years, but fuel buildup was not evident.

The burn history of the stand in the years before 1960 is unknown, but, since then, it has burned twice; once in August of 1984 and again in August of 1987. Both fires burned entirely through the stand, as well as hundreds of hectares immediately surrounding the stand area, after originating at locations several kilometers from the stand. Both fires were moved fast enough by winds to thwart fire suppression efforts. Actual stand burning was not witnessed.

The information for this report was obtained from four permanent study plots, each 3 x 15 m (45 m²), that had been established in the buckwheat stand in 1983, the year before the first wildfire, and all the living shrubs were counted. The living plants were again counted in May of 1985, 1986, and 1988. Characteristically, round-headed buckwheat plants flower in May. Some

leaves remain attached to twigs through the summer, but many have dropped by August and the plants are visibly moisture stressed.

Results and Discussion

The number of living round-headed buckwheat plants on the study plots before burning averaged 59.75 shrubs per plot (Table 1). In the first growing season following the first burning, counts averaged 21.25 plants per plot. Only one of the surviving shrubs had flowered and it was the only shrub on the study plots that had no visible burn damage. In the second growing season, six additional living shrubs were counted indicating that some of the burn damaged shrubs thought to be dead were eventual survivors. Of the 91 surviving plants, 89 were in flower in the second growing season indicating that burn damaged plants were able to restore reproductive vigor. Following the second burning, the number of living shrubs was reduced to an average of 3.25 plants per plot (Table 1).

A conclusion is that, although buckwheat shrubs are vulnerable to summer burning, they do have some capacity to recover from burning that damages more than one-half of the plant canopy. The only protection the shrubs have against wildfire is low stand density coupled with low fuel potential of the understory herbs.

Although the buckwheat stand has burned twice in a four year period, some shrubs on the outcrop have not been touched by fire. It was estimated that about 5 percent of the shrubs in the stand were not burned by either fire. These shrubs and those that recovered from burn damage are the seed sources for future buckwheat recolonization of the outcrop. It is important for at least a few shrubs to survive burning because rocky outcrops are isolated from one another, making natural seed transport from one outcrop to another difficult.

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TABLE 1. Counts of living round-headed buckwheat shrubs on four 3 x 15 m study plots in the year 1983 (pre-burn) and in the post-burn years 1985, 1986, and 1988.

Year	Plot 1	Plot 2	Plot 3	Plot 4	Mean	Density per 100 m ²
1983 (Pre-burn)	56	48	77	58	59.75	132.8
1985 (first season after burning)	15	12	37	21	21.25	47.2
1986 (second season after burning)	16	12	42	21	22.75	50.6
1988 (first season after second burning)	1	4	5	3	3.25	7.2

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Warm Pretreatment Effects on Antelope Bitterbrush (*Purshia tridentata*) Germination Response to Chilling

Abstract

Antelope bitterbrush occurs over a wide range of habitats in the West, yet laboratory germination requirements for fresh seed collections are remarkably similar. The seeds are dormant when dispersed in midsummer and require four to six weeks of moist chilling to become germinable. Laboratory experiments were conducted to test the hypothesis that warm dry summer conditions at low elevation sites would tend to make seeds less dormant at the beginning of winter chill, while warm moist conditions at higher elevation sites would tend to lengthen the winter chill required to break dormancy. Warm-dry seed pretreatments for short periods (4-8 weeks) at moderate temperature (15 and 30°C) significantly increased germination response to an otherwise inadequate (2-week) chill. Warm-moist seed pretreatments (2 weeks at 15 or 30°C) significantly decreased germination response to an otherwise adequate (4-week) chill. These results suggest that conditions experienced during summer and fall by rodent-cached antelope bitterbrush seeds in the field may change their chill requirements. The resulting increased dormancy at sites with longer winters and decreased dormancy at sites with shorter winters would increase the chances for correctly timed emergence and thus for seedling survival in different habitats. These findings have implications for artificial seeding of antelope bitterbrush, since conditions experienced in dry storage prior to fall seeding may be different from postdispersal conditions in the field.

Introduction

Antelope bitterbrush (*Purshia tridentata*) is an important shrub species in the restoration of depleted big game habitat through artificial seeding (Tiedemann and Johnson 1983). Its germination and establishment ecology have been the subject of numerous studies (Basile and Holmgren 1957, Sherman and Chilcote 1972, Young and Evans 1976, Evans and Young 1977). Seeds ripen from June to August, depending on habitat type, with populations at warmer, drier lowland sites maturing seed first. The seeds are completely dormant at the time of dispersal and require a period of moist chilling to become germinable (Young and Evans 1976). The dormancy is coat-imposed, since excised embryos germinate readily (Nord 1956). Dormancy serves to postpone emergence until late winter/spring, when reduced risk from frost coincides with favorable soil moisture for seedling establishment. The large seeds are a preferred food of rodents and are quickly gathered, stripped of their pericarps, and cached after dispersal from the plant (Sherman and Chilcote 1972, Everett *et al.* 1978, Evans *et al.* 1983). Most seedling emergence under natural conditions is from rodent caches (Sanderson 1962, West 1968).

Antelope bitterbrush occurs over a wide range of habitats (Hormay 1943, Nord 1965). It may dominate warm summer-dry shrublands along the

Columbia River, where annual precipitation is less than 250 mm. It occurs as the understory dominant in ponderosa pine and lodgepole pine forests with heavy winter snowpack. It also has a wide geographic range, occurring in predominantly winter precipitation areas in the Northwest and in California but also in summer precipitation areas of the Southwest.

Because of its great ecological amplitude, one might expect antelope bitterbrush seed germination requirements to vary from one population to another and to be correlated with salient climatic features of the habitat. Such climate-correlated variation in germination pattern and more specifically in the chill requirement for breaking dormancy has been found in other genera of woody Rosaceae (Westwood and Bjornstad 1968, Kester 1969, Barclay and Crawford 1984). The concept of ecotypic differentiation in germination strategy for species of wide ecological amplitude is generally well accepted (Thompson 1981).

In contrast with these examples, seed collections of antelope bitterbrush from contrasting habitats show remarkably little variation in germination characteristics, and the variation that does exist is not correlated in any intuitively obvious way with habitat characteristics (Meyer and Monsen 1989). Researchers working with antelope bitterbrush seedlots have generally found that

a four-week chill is adequate to break dormancy in most or all of the seeds in a lot, regardless of provenance (McConnell 1960, McHenry and Jensen 1967, Young and Evans 1976). This relative lack of variation between seed collections is puzzling, and prompted the experiments reported here.

Because antelope bitterbrush seeds are dispersed in midsummer, they spend a considerable time (2 to 5 months) in the dormant state prior to the beginning of field chilling, which requires a coincidence of soil temperatures between -2° and 5°C with high levels of soil moisture (Young and Evans 1981). The seeds are nongerminable prior to chill, but this does not mean that their level of dormancy (as measured by their response to chilling) remains constant. The hypothesis tested here is that seeds which experience warm, dry conditions during this summer-fall period will become less dormant, while those which experience warm, moist conditions will become more dormant. This would mean that seeds at warm, dry sites, which are less likely to provide long chill periods, would be less dormant at the beginning of chill than at the time of dispersal. Seeds at higher elevation sites would be more likely to spend part of the summer-fall period imbibed and thus would be more dormant at the beginning of the chill period than at the time of dispersal. These sites would in turn be able to provide longer chill periods. These predictions are based on earlier observations showing (1) that bitterbrush seeds dry-afterripen, i.e., become less dormant in dry storage, and (2) that bitterbrush seeds whose chill period is interrupted by a warm-moist treatment become more dormant, i.e., require a longer total chill period to break dormancy (Meyer and Monsen 1989).

In the present work, antelope bitterbrush seeds were subjected to various warm-moist and warm-dry pretreatments, and the effect of these pretreatments on response to chill was observed.

Methods

Seed collections were made in the summers of 1986 and 1987. The seeds were hand-threshed on a rubbing board to remove the papery pericarps, cleaned in a table model fanning mill, and stored in manila envelopes under laboratory conditions (20° to 22°C , 7 to 9% moisture content) until use. Seeds used in the experiments were hand-selected

to eliminate shrivelled, insect-damaged, or otherwise unsound seeds.

For each experimental treatment, four replications of 25 seeds each were used. Seeds were incubated in 100 mm plastic petri dishes between two standard germination blotter disks kept moist as necessary. Radicle protrusion to 5 mm was the criterion for germination. Completely randomized experimental designs were used.

1986 Seed Experiment

In the first experiment five 1986 collections were used which were approximately 12 months old at test initiation (Table 1). Experiments on these lots at 2 and 10 months of age have been reported elsewhere (Meyer and Monsen 1989). A factorial combination of warm-imbibed and warm-dry pretreatments and chill treatments was used. Warm pretreatments were carried out for two weeks in darkness at either 15° or 30°C . For the dry pretreatments, dry seeds were placed in unsealed petri dishes, while for the imbibed pretreatments the seeds were placed between moistened blotters as described above. At the end of the warm pretreatment period, dry seeds were also placed between moistened blotters, and the chill periods were initiated. Seeds were chilled in darkness at 1°C in order to simulate conditions under snowpack for two weeks and for four weeks. No germination occurred during chilling. At the end of the chill treatments, seeds were placed in darkness at 15°C for two weeks and germination percentages were recorded.

Seeds remaining at the end of the germination period were examined using tetrazolium staining techniques to determine viability. The imbibed seeds were slit open at the cotyledon end, and the embryos were excised by squeezing and immersed in a buffered 1 percent solution of tetrazolium chloride for 24 hours at room temperature. They were then evaluated according to established procedures (Grabe 1972).

1987 Seed Experiment

In the second experiment, six 1987 seed collections were used (Table 1). Tests were started approximately two months after harvest. Four replications of 25 seeds from each collection were tested for initial viability using tetrazolium staining techniques as described above. Air-dry seeds

TABLE 1. Collection information and initial viability percentage (ITV) estimated using tetrazolium staining techniques for antelope bitterbrush seed accessions used in the study.

Accession	Year	ITV	Lat	Long	Alt (m)
Celilo	OR 1986	90	45°38'N	120°58'W	120
Middleton	ID 1986	87	43°49'N	116°40'W	770
Reynolds					
Creek	ID 1986	98	43°07'N	116°46'W	1510
St. Anthony	ID 1986	95	44°03'N	111°57'W	1780
Red Canyon	UT 1986	97	37°43'N	112°16'W	2430
Stansbury					
Mtn.	UT 1987	97	40°33'N	112°35'W	1840
Wells	NV 1987	96	41°07'N	114°48'W	1850
Ftn. Green	UT 1987	86	39°37'N	111°37'W	1850
Pinto	UT 1987	96	37°32'N	113°32'W	1860
Ruby Valley	NV 1987	98	40°40'N	115°27'W	1910
Lake Mtn.	UT 1987	95	40°15'N	111°57'W	2220

of each collection were placed in sealed vials and subjected to a series of six warm-dry pretreatments. Preliminary trials showed that seed moisture loss from the sealed vials was negligible. The dry pretreatments were two and four weeks at 50°C, two, four and eight weeks at 30°C, and eight weeks at 15°C. A control treatment in which seeds were placed directly into chill with no additional dry storage period was also included. At the end of each dry pretreatment, seeds were counted into petri dishes, placed between moistened blotters and subjected to one of four chill treatments. These treatments were no chill, two or four weeks of chill at 1°C, or a two-week period imbibed at 15°C followed by a four-week chill. No germination occurred during chilling. At the end of each chill period, seeds were incubated at 15°C for two weeks and germination percentages were recorded. Since the four-week 50°C pretreatment was the only treatment suspected of causing any loss of viability, four replications of 25 seeds of each collection from this treatment were evaluated using tetrazolium staining techniques as described earlier.

The data from each experiment were arcsine transformed for analysis of variance. The Student-Newman-Keuls means separation test was used to evaluate the significance of differences between means. In the first experiment, germination percentage in each experimental unit (petri dish) was expressed as a percentage of total viable seeds in that unit. In the second experiment, initial viability percentage for each collection as

determined by tetrazolium staining was included as an additional treatment value for comparison in the analysis.

Results

1986 Seed Experiment

Seeds exposed to two-week dry pretreatments at 15° and 30°C showed nearly identical responses to two or four weeks of chill (Figure 1). Averaged across collections, germination after the four-week chill was 94 percent, while germination after the two-week chill averaged 42 percent. In contrast, seeds exposed to two-week warm pretreatments while imbibed showed a marked decrease in response to both two and four weeks of chill when compared with dry pretreated seeds (Figure 1). Imbibed pretreatment at 15°C was almost as effective as the 30°C pretreatment in increasing dormancy.

Seeds from Red Canyon, Utah, were the least dormant, while seeds from Celilo, Oregon, and Middleton, Idaho, were the most dormant, a result similar to those reported for these lots in earlier experiments (Meyer and Monsen 1989). Reduction in germination response to a two-week chill as a consequence of imbibed warm-pretreatment compared to a dry warm-pretreatment was greater for high elevation northern collections, while reduction in response to a four-week chill was greater for low elevation collections (Table 2).

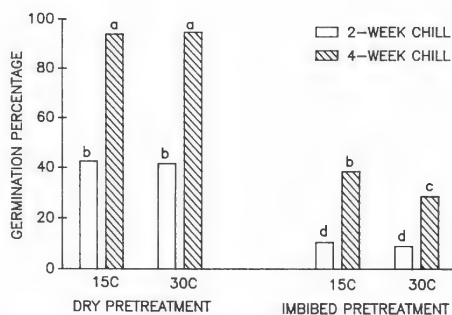


Figure 1. Treatment effects (averaged across seed accessions) in the factorial experiment combining 15° and 30°C dry and imbibed 2-week pretreatments with 2- and 4-week chill treatments. Seeds were incubated at 15°C for 2 weeks following chilling. Bars headed by the same letter represent means not significantly different at the $p < .05$ level.

TABLE 2. Effect of factorial combinations of warm pretreatments and chill treatments on relative germination percentage for 5 antelope bitterbrush seed accessions collected in 1986. Within an accession (row), means followed by the same letter are not significantly different at the $p < .05$ level.

Accession		2-week moist chill (percentage)				4-week moist chill (percentage)			
		Imbibed		Dry		Imbibed		Dry	
		15°C	30°C	15°C	30°C	15°C	30°C	15°C	30°C
Celilo	OR	6d	8cd	22bc	26b	20bcd	18bcd	80a	88a
Middleton	ID	8b	9b	14b	12b	16b	15b	94a	87a
Reynolds Creek	ID	9c	5c	49b	47b	43b	40b	100a	99a
St. Anthony	ID	4e	11de	48b	35bc	41bc	20cd	96a	100a
Red Canyon	UT	24d	13d	80b	88b	74b	49c	100a	100a

1987 Seed Experiment

In the second experiment, warm dry pretreatments were largely ineffective in eliminating the chill requirement of fresh seeds (Figure 2A). Some warm pretreatments significantly affected germination response to a two-week chill (Figure 2B). The two-week pretreatments at 30° and 50°C were not significantly different from the control percentage value. Four weeks at 30°C gave the highest germination percentage, a value nearly double the control value. However, extending the 30°C pretreatment to eight weeks did not result in further dormancy reduction. Storage at 15°C for eight weeks resulted in a significant germination increase relative to the control, while storage at 50°C for four weeks gave a significant decrease.

Differences among warm pretreatments became relatively insignificant when seeds were subjected to four weeks of chill, because a four-week chill was effective in breaking most of the dormancy even in the control (Figure 2C). A slight but significant increase over the control value was seen after four and eight weeks of storage at 30°C.

A notable exception to the above trend was the sharp decrease in response to a four-week chill after four weeks of storage at 50°C. This reduction was due mostly to some sort of secondary dormancy induction and not to reduced viability of the seeds (Table 3). Different collections showed different degrees of sensitivity to the four-week 50°C treatment. Reduction in response to a four-week chill ranged from 23 to 79 percent (Table 3).

A fourth chill treatment was included to find out if warm dry pretreatments would change the effect of a two-week imbibed pretreatment at 15°C on response to chill. This treatment (2

weeks imbibed at 15°C) greatly decreased the response of one-year-old seed collections to a four-week chill in the first experiment. Averaged across collections in the second experiment, the two-week 15°C imbibed pretreatment decreased the control response to a four-week chill from 93 to 55 percent (Figure 2C, 2D). Warm dry pretreatments generally ameliorated the dormancy-inducing effects of the 15°C imbibed pretreatment (Figure 2D). Longer and warmer dry pretreatments were more effective. This included the four-week 50°C pretreatment, which had a mean germination percentage of 74 after the warm imbibed/chill treatment sequence, a value not significantly different from the maximum. This is a puzzling result, since this pretreatment followed directly by a four-week chill resulted in only 48 percent germination. The warm imbibition period apparently overcame whatever dormancy-inducing effects had been imposed by the high temperature dry pretreatment, even though it tended to induce dormancy in seeds not exposed to the high temperature pretreatment.

Different collections responded quite differently to this series of treatments (Table 3). The Lake Mountain collection once again was most dormant, with the greatest depression in response to four-week chill as a result of the warm imbibition treatment and little ameliorating effect from the four-week 50°C dry pretreatment. The Pinto collection was again least dormant and was little affected by the warm imbibition treatment.

Discussion

A period of warm-imbibition prior to the beginning of chill increased dormancy for all seed accessions in both experiments. These results

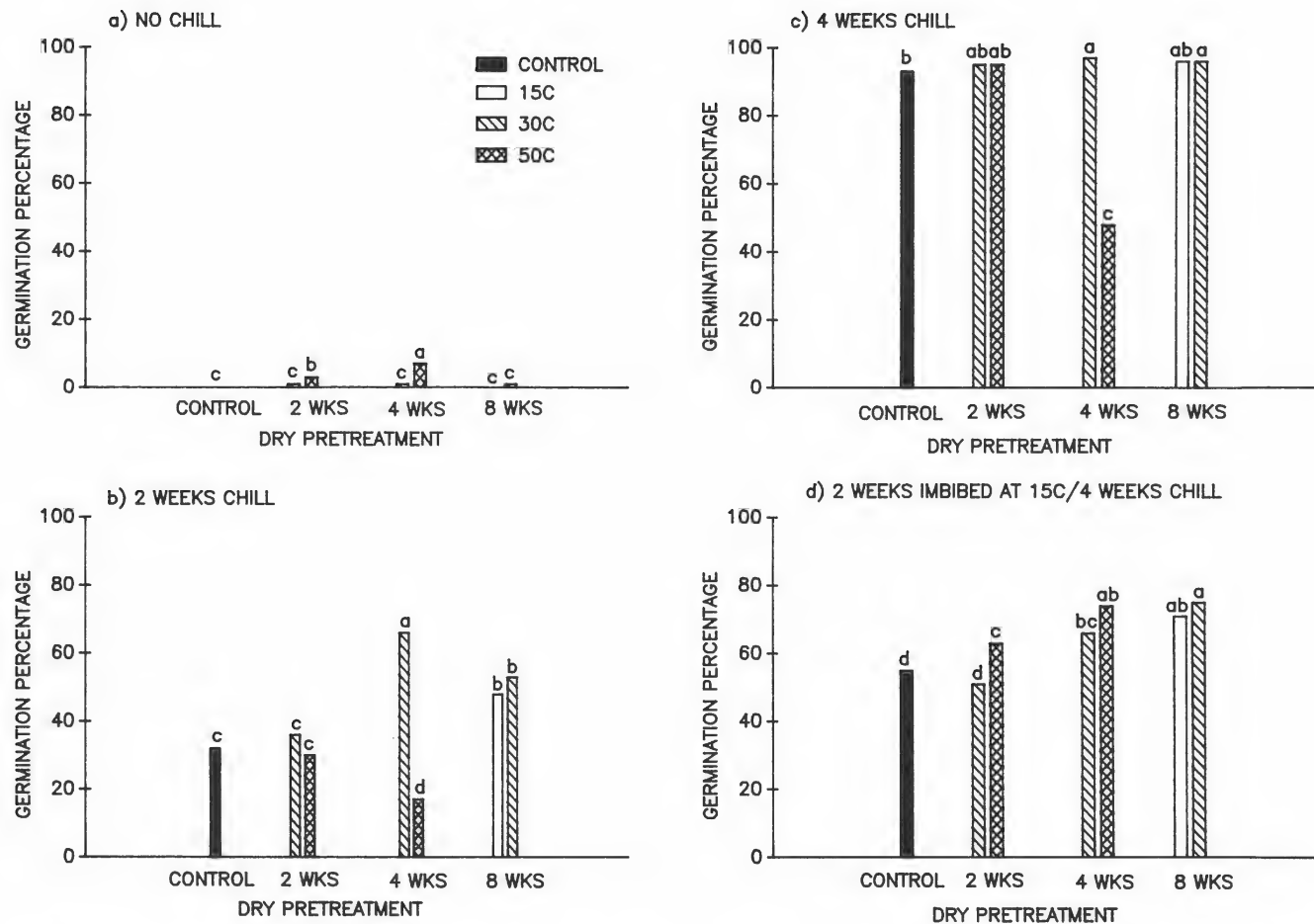


Figure 2. Dry pretreatment effects (averaged across seed accessions) for each of 4 chill treatments: (a) no chill, (b) 2-week chill, (c) 4-week chill, (d) 2 weeks at 15°C followed by a 4-week chill. Seeds were incubated at 15°C for 2 weeks following chill treatments. Within a chill treatment, bars headed by the same letter represent means not significantly different at the $p < .05$ level.

TABLE 3. Effect of a 4-week, 50°C dry pretreatment on response to chill treatments for six antelope bitterbrush seed accessions collected in 1987. Chill treatments are 0, 2, and 4 weeks at 1°C, and 2 weeks imbibed at 15°C (2-week prewarm) followed by 4 weeks at 1°C. Control values (Ctr) are for seeds not subjected to a dry pretreatment. Initial total viable seed percentage (ITV) is included for comparison. Within an accession (row), means followed by the same letter are not significantly different at the $p < .05$ level.

Accession	Chill period (Germination percentage)									
	ITV		0-week		2-week		4-week		4-week (2-week pw)	
	Ctr	4/50	Ctr	4/50	Ctr	4/50	Ctr	4/50	Ctr	4/50
Stansbury Mtn.	98a	96a	0e	4e	25d	21d	96a	44c	65bc	81b
Wells	99a	92ab	0e	14d	53c	20d	97a	56c	52c	84b
Ftn. Green	89a	83a	0d	3d	30c	17c	86a	59b	59b	58b
Pinto	97a	95a	0f	16e	40c	29d	99a	76b	86b	82b
Ruby Valley	99a	96a	0f	3f	24d	10e	90b	41d	39d	73c
Lake Mtn.	99a	91b	1f	1f	22de	2f	92b	13e	28d	63c

support the hypothesis that periods spent in the imbibed state prior to the beginning of chilling in the field would increase the chill period necessary for elimination of dormancy. Processes that operate to reduce dormancy during chilling are known to be reversible at warm temperatures for seeds of many cold temperate woody species including other Rosaceae (Stewart and Semeniuk 1965, Nikolaeva 1977). The ecological significance of this phenomenon has apparently not been previously addressed.

Warm-dry pretreatments significantly affected the response to chill for all six fresh seed accessions tested, but these effects were not unidirectional. In general, treatments of intermediate length and at intermediate temperatures tended to make the seeds less dormant. But when either temperature or time periods were increased, the effect was reversed. The physiological processes which underlie these changes in dormancy are unknown. In traditional seed physiology, rate of dry-afterripening (dormancy reduction in dry storage) is considered to be directly related to temperature of storage, and reports of increased dormancy in dry storage under any conditions are difficult to find (Bewley and Black 1982). Dry pretreatments in this experiment were carried out in sealed vials to maintain the seeds at a constant moisture content. Under field conditions, seeds would tend to lose moisture at high temperatures. This might obviate both the afterripening and the dormancy induction effects observed here, because physiological processes in "dry" seeds require a minimum moisture content to proceed (Bewley and Black 1982).

Seeds on the soil surface in bitterbrush habitats may experience temperatures in excess of 50°C, but the mean temperature would certainly be much lower (Ferguson 1972). In a rodent cache only a few centimeters beneath the surface, extremes would be greatly damped by the insulating effects of soil. Thus, the effect of 50°C constant temperature may not have much field relevance unless the seeds are unburied and the dormancy-inducing effects of high temperature are cumulative.

The case for 30°C as a mean summer temperature inside a rodent cache is easier to make, at least for low elevation sites where dry-afterripening is likely to be more important. The temperature for dry-afterripening may not have to be high for the seeds to undergo significant dormancy reduction. This is indicated by the significant effects of eight weeks of storage at 15°C, a temperature probably well below the summer mean in rodent caches.

The experimental results suggest a complex response to temperature by seeds in the dry state. In general the dormancy reduction at moderate temperature over several weeks supports the hypothesis that dry-afterripening in the field would decrease the level of dormancy at the beginning of chill.

Another result with possible ecological relevance is the fact that warm-dry pretreatments had a significant ameliorating effect on the induction of dormancy in the warm-imbibed state. Summer dry-afterripening may function to prevent dormancy induction in the imbibed state

during fall storms. This effect could be as important as direct reduction of dormancy. Even the highly dormancy-inducing four-week 50°C dry pretreatment interacted synergistically in some way with the warm-imbibed treatment to result in a net reduction in dormancy relative to the control.

Without knowing more about temperature and moisture conditions inside rodent caches in various types of antelope bitterbrush habitat, it is unwise to speculate further on the ecological significance of the present results. But the laboratory experiments indicate that field studies on seed dormancy in antelope bitterbrush could yield interesting results. The present findings may also have some practical implications for managers involved in artificial seeding with antelope bitterbrush. Bitterbrush seed is known to retain its viability through many years of storage (Stevens *et al.* 1981). But the effects of storage, and more particularly of storage temperature, on degree of seed dormancy have rarely been considered. Storage of freshly harvested seeds could have indirect effects as well. The normal practice in seeding bitterbrush is to seed as late in the fall as possible to avoid rodent

depredation, a major deterrent to seeding success (Stephen B. Monsen, pers. comm.). This places the seed in the ground roughly at the beginning of the field chilling period, so that processes that would occur in the field between dispersal and chill initiation are largely circumvented. Direct and indirect effects of seed storage and sowing time could condition a response to chill which is inappropriate at the seeding site and result in failure of the seeding. We do not yet know how to predict or manipulate these effects. But continued investigation of germination biology with a focus on field aspects will add to our knowledge of this useful and important wildland shrub.

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Studies in *Sidalcea* Taxonomy

Abstract

The objectives of this study were to investigate taxonomic relationships among the four species of *Sidalcea* growing in Oregon's Willamette Valley, and among various populations of *Sidalcea nelsoniana*. These relationships were assessed by examining pollen with the scanning electron microscope, and performing principal component analysis (PCA) on gross morphological features of the plants. Pollen morphology was of limited use in making intra- and inter-specific comparisons. Chromosome number was determined for six populations of *S. nelsoniana*; it was identical for all populations ($n = 10$). PCA was useful in segregating the four *Sidalcea* species. However, a PCA of 73 specimens of *S. nelsoniana* revealed no distinct sub-taxa; this information is useful in making management decisions for this Category 2 candidate species.

Introduction

Sidalcea is comprised of herbaceous annuals and perennials native to western North America (Roush 1931, Hitchcock 1957). The four species found in the Willamette Valley of Oregon, *S. nelsoniana* Piper (Nelson's checker-mallow), *S. cusickii* Piper (Cusick's checker-mallow), *S. campestris* Greene (meadow sidalcea), and *S. virgata* Howell (rose checker-mallow), are all perennials that bloom in late spring to mid-summer and are characterized by a gynodioecious breeding system. In a gynodioecious species individual plants are either pistillate (the flowers are male-sterile) or hermaphroditic (the flowers are perfect). Often morphological differences, such as overall plant size or flower size (Willson 1983), can be found between these two types of individuals. The existence of these two different morphological types within a species has resulted in frequent misidentification of these species. Therefore, the primary goal of this study was to clarify species relationships by examining selected taxonomic and morphologic characteristics of these species.

The taxonomy of *S. nelsoniana*, a western Oregon endemic, has been a concern to federal agencies as it is a candidate species for federal listing as a Category 2 species (U.S. Fish and Wildlife Service 1985). It is found in the northern Coast Range in both the Nestucca River and the Wilson River drainages, and in the Willamette Valley from Benton and Linn Counties north to Washington County (Halse and Glad 1986). The

existence of *S. nelsoniana* in these two different habitats has led to speculation that there may be two separate taxa. This paper also examines this hypothesis.

The proposed construction of a water supply reservoir at Walker Flat in the Coast Range, west of Carlton, would inundate an area which currently supports a large population of *S. nelsoniana* (Glad *et al.* 1987). Determining the taxonomic status of the *S. nelsoniana* at Walker Flat would help federal agencies assess the significance of managing this population.

Materials and Methods

Relationships among the four species of *Sidalcea*, and within *S. nelsoniana*, were determined by examination of pollen with a scanning electron microscope (SEM), and principal component analysis (PCA) of selected morphological characteristics. In addition, chromosome counts were made for six *S. nelsoniana* populations, two from the Coast Range and four from the Willamette Valley.

Air dried pollen collected from the four species of *Sidalcea* was dispersed on 15 mm diameter coverslips coated with a thin adhesive film (Mikrostick). Coverslips were attached to aluminum planchets using conductive silver paint. After mounting, specimens were coated with approximately 150 Å of 60:40 weight percent Au/Pd alloy in a Varian VE-10 vacuum evaporator at a vacuum of 1×10^{-5} Torr. Examination was made using an AMRAY 1000 A SEM, operated at 10 or 20 kV, at the Electron Microscope Facility, Department of Botany and Plant Pathology, Oregon State University. Images were

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recorded on Polaroid Type 55 positive/negative 4 x 5 format film.

For chromosome determination, floral buds from six populations of *S. nelsoniana* were collected in the field and fixed in a modified Carnoy's solution (4 chloroform: 3 ethanol: 1 glacial acetic acid, v/v/v). Acetocarmine squashes of pollen mother cells were obtained by using the technique of Snow (1963).

The morphological measurements for this study were obtained from 131 herbarium specimens of the four species of *Sidalcea* borrowed from the herbaria at Oregon State University, the University of Oregon, Washington State University, the University of Washington, Willamette University, and the United States Fish and Wildlife Service, Boise, Idaho. Of these specimens 73 were of *S. nelsoniana*, 22 of *S. campestris*, 21 of *S. virgata* and 15 of *S. cusickii*. Specimens were from throughout the species' distribution in the Willamette Valley. A list of the specimens, and their site localities, used in the PCA is available from the senior author on request.

The five morphological parameters listed in Table 1 were measured on all 131 herbarium specimens. Only those specimens which had all five morphological parameters were used in the PCA. These parameters were selected for the PCA because they are considered to be important traits in the latest monograph of the genus (Hitchcock 1957) and are traits emphasized in the latest regional flora (Hitchcock and Cronquist 1973). Sixteen morphological characters were initially examined (CH2M Hill 1986). Many of these characters were judged to be so similar among species as to be non-discriminating and were not included in the investigation (e.g., calyx pubescence, flower density, upper stem pubescence, style number). Other characters, while important taxonomically, are usually not found on most herbarium specimens (e.g., root type, fruit traits).

Examination of the herbarium specimens revealed that the flowers on the perfect-flowered plants tended to be larger than the flowers on the pistillate-flowered plants. The influence of sex on the parameters used in the PCA was tested using a factorial analysis of variance (ANOVA) with flower sex and species as the factors. The number of specimens of each species and flower type are indicated in Table 2. This analysis indicated a significant effect of flower sex and

TABLE 1. Definition of morphological parameters used in *Sidalcea* principal component analyses.

Abbreviation	Definition	Numeric Code
BASTPU	basal stem pubescence	1 = none 2 = simple 3 = forked or stellate
PETCOL	petal color	1 = white or pink 2 = red, lavender or purple
ADPETLG	adjusted petal length	millimeters
ADCALLG	adjusted calyx length	millimeters
CALCOL	calyx color	1 = green 2 = green with some purple 3 = purple

species on the length of the petals and calyces. Therefore, for the PCA, the length of the petals and calyces were adjusted for sex-related flower differences. For both petals and calyces, this adjustment was made separately for each species by adding the difference between the mean length of the perfect-flowered specimens and the mean length of the pistillate-flowered specimens to each of the pistillate-flowered individuals. Following this adjustment, the mean length of the pistillate-flowered individuals was equal to the mean length of the perfect-flowered individuals. This eliminated segregation of individuals based solely on the sex of the flower. Data on the five parameters listed in Table 1 for *S. nelsoniana*, *S. virgata*, *S. cusickii* and *S. campestris* were analyzed by a PCA computer program (SAS Institute Inc. 1985). The raw data from the specimens used in this analysis are summarized in Table 2.

Following the PCA of the four species, a PCA was performed on 73 specimens of *Sidalcea nelsoniana* alone, in order to examine the relationship between the specimens found in the Coast Range, particularly those from Walker Flat, and those of the Willamette Valley.

Results and Discussion

The pollen of all specimens of *Sidalcea* is typically malvaceous (Figure 1). The grains are 60-70 microns in diameter, are conspicuously spiny, have a granular surface and are pantoporate.

TABLE 2. Means and standard deviations of morphological parameters for *Sidalcea* species analyzed in the principal component analysis.

Species	Flower Sex	Parameter ¹					
		n	BASTPU	PETCOL	PETLG	CALLG	CALCOL
<i>S. nelsoniana</i>	Perfect	41	2.0 ± 0.3	2.0 ± 0.0	11.5 ± 2.0	5.5 ± 0.7	2.0 ± 0.2
	Pistillate	32	2.0 ± 0.2	2.0 ± 0.0	7.1 ± 1.3	4.7 ± 0.7	2.0 ± 0.2
<i>S. virgata</i>	Perfect	11	3.0 ± 0.0	2.0 ± 0.0	19.8 ± 3.6	8.7 ± 1.4	1.7 ± 0.5
	Pistillate	10	2.9 ± 0.3	2.0 ± 0.0	10.6 ± 1.5	6.3 ± 1.2	1.8 ± 0.4
<i>S. cusickii</i>	Perfect	8	2.5 ± 0.9	1.9 ± 0.4	14.5 ± 3.5	7.8 ± 2.0	1.9 ± 0.4
	Pistillate	7	3.0 ± 0.0	2.0 ± 0.0	9.7 ± 1.7	6.9 ± 0.8	1.8 ± 0.4
<i>S. campestris</i>	Perfect	15	2.1 ± 0.4	1.1 ± 0.2	17.3 ± 4.6	7.5 ± 1.3	1.7 ± 0.5
	Pistillate	7	2.0 ± 0.0	1.0 ± 0.0	10.2 ± 0.7	6.1 ± 0.7	1.6 ± 0.5

¹See Table 1 for definitions of parameters.

The smooth, sticky surface material covering at least part of the granular surface (Figure 1-C,E) is due to the presence of pollenkit (Dobson pers. comm.), which has been reported from other species of *Sidalcea* (Dobson 1988). Although the pollen of *S. campestris* exhibits some variability in size and shape of the spines, the pollen grains of all the taxa are very similar and do not appear to be useful taxonomically.

The number of chromosomes in all six of the *S. nelsoniana* populations that were examined were identical ($n = 10$). The specimens counted were *Halse 3178*, *3312* (Yamhill County, Walker Flat), *Halse 3313* (Tillamook County, Devils Lake Fork of the Wilson River), *Halse 3289*, *3293* (Benton County, Corvallis), *Halse 3240* (Polk County, Rickreall), *Halse 3291* (Marion County, Turner). This count is consistent with an earlier report (Kruckeberg 1957). *S. nelsoniana*, like *S. cusickii*, shows no signs of polyploidy, although polyploidy is found in both *S. campestris* ($2n = 60$) and *S. virgata* ($2n = 20$ or 40) (Kruckeberg 1957).

The results of the ANOVA indicate that there is a statistically significant difference ($p < 0.001$) among species for all of the five parameters listed in Table 1, indicating that all of them are useful in distinguishing among species. The ANOVA also indicates statistically significant ($p < 0.001$) differences in petal length and calyx length between the perfect-flowered and pistillate-flowered plants of the same species. There is also a significant difference attributable to the species-by-flower sex interaction for the petal length ($p < 0.01$) and the calyx length ($p < 0.05$). This in-

dicates that the magnitude of the effect of flower sex on petal and calyx length varies among species (Table 2).

The first two components of the PCA for the four species of *Sidalcea* account for 70.6 percent of the total variation, and are plotted in Figure 2. The eigenvectors for each component are listed in Table 3. In general, there is an observable separation between *S. nelsoniana* in the left-central section of the plot, *S. campestris* in the right-lower section, and *S. virgata* in the right-upper of the figure. *S. cusickii* is less clearly segregated from the other species, and intermingles extensively with *S. virgata* and somewhat with *S. nelsoniana*. These results suggest that, with the exception of *S. cusickii*, the characters used in the PCA are generally effective and appropriate for distinguishing between the four species of *Sidalcea* used in this study. The third, fourth and fifth components were examined (plots are not shown) and these also failed to provide a clearcut segregation between *S. virgata* and *S. cusickii*. However, *S. cusickii* and *S. virgata* have some distinguishing fruit and calyx characters not used in this study (e.g., calyx venation and shape, carpel reticulation).

One of the problems in identifying species of *Sidalcea* from the Coast Range and Willamette Valley is that the keys and species descriptions in both Hitchcock's monograph (1957) and local floras do not distinguish petal and calyx length differences associated with flower sex. Generally the petal length, and calyx length, is simply given as the combination of the lengths of both sexes; i.e., in *S. nelsoniana* petal length is given

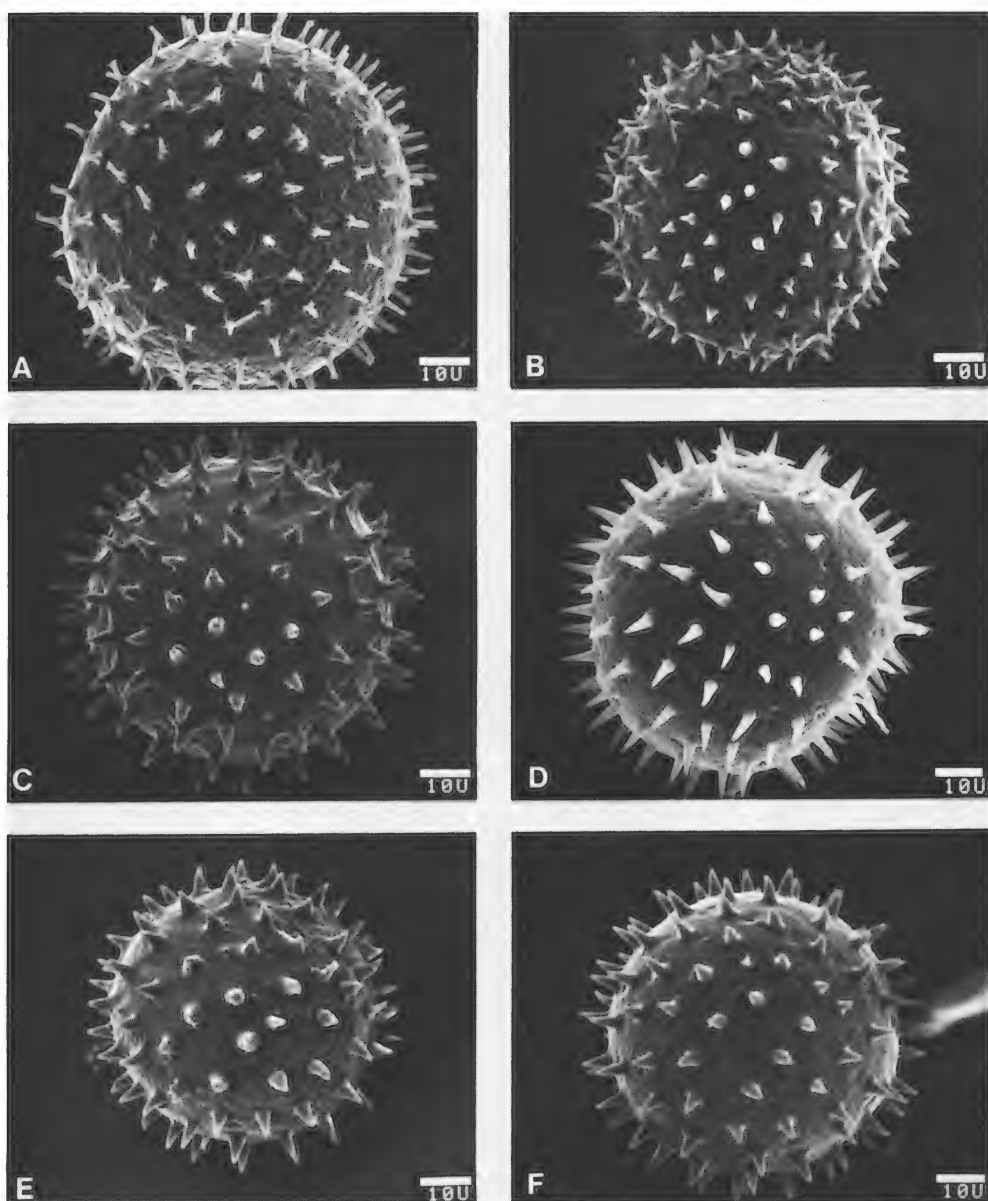


Figure 1. Scanning electron photomicrographs of *Sidalcea* pollen. A, *S. campestris*, Polk Co.: Highway 22, Rickreall, Halse 3299; B, *S. campestris*, Linn Co.: Cogswell-Foster, Halse 3455; C, *S. virgata*, Benton Co.: Smith Loop Road, south of Corvallis, Halse 3281; D, *S. cusickii*, Douglas Co.: Calapooia Valley, Cole s.n.; E, *S. nelsoniana*, Yamhill Co.: Walker Flat, Halse 3312; F, Polk Co.: Rickreall, Halse 3290. (Voucher specimens at Oregon State University).

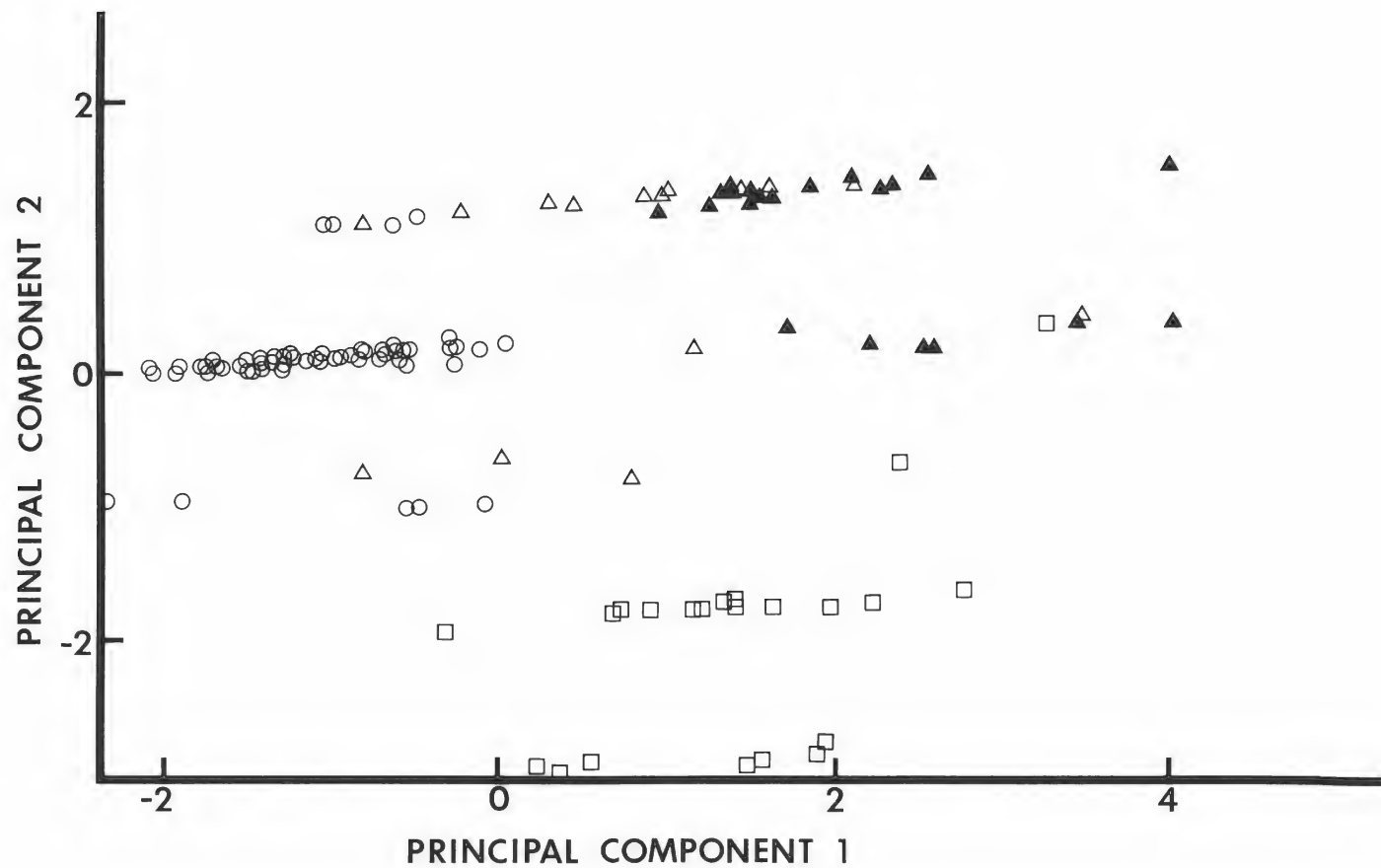


Figure 2. The first two principal components for specimens of *Sidalcea* species. *S. nelsoniana* (○), *S. virgata* (▲), *S. cusickii* (△) and *S. campestris* (□).

TABLE 3. Eigenvectors for morphological parameters in each component of the principal component analysis of four species of *Sidalcea*.

Parameter ¹	Component				
	1	2	3	4	5
BASTPU	+0.397	+0.542	-0.259	-0.693	-0.032
PETCOL	-0.241	+0.743	-0.277	+0.539	+0.148
CALCOL	-0.275	+0.376	+0.864	-0.185	-0.043
ADPETLG	+0.599	+0.000	+0.271	+0.208	+0.724
ADCALLG	+0.591	+0.114	+0.189	+0.388	-0.672
Variance					
Explained	46.7%	23.9%	17.1%	9.3%	3.0%

¹See Table 1 for definitions of parameters.

1. Petals white to pink; basal stem pubescence simple; petals of perfect flowers 13-25 mm long, calyx 6-9 mm long; petals of pistillate flowers 9-12 mm long, calyx 5-7 mm long. *S. campestris*
1. Petals red, lavender or purple
 2. Basal stem pubescence simple; petals of perfect flowers 9-15 mm long, calyx 4.5-7 mm long; petals of pistillate flowers 5-9 mm long, calyx 4-6 mm long. *S. nelsoniana*
 2. Basal stem pubescence of forked to stellate hairs
 3. Petals of perfect flowers 11-19 mm long, calyx 6-10 mm long; petals of pistillate flowers 8-12 mm long, calyx 6-8 mm long; calyx usually prominently veined, lobes widened above base, $\pm$ ovate-lanceolate. *S. cusickii*
 3. Petals of perfect flowers 15-25 mm long, calyx 7-10 mm long; petals of pistillate flowers 9-13 mm long, calyx 5-7 mm long; calyx not prominently veined, lobes not widened above base, tapered evenly to the tip. *S. virgata*

The PCA using the five characters examined on 73 specimens of *S. nelsoniana* shows no component separation among geographical populations of this species. The first two components of the PCA for *S. nelsoniana* are plotted in Figure 3. The total variation in component 1 is similar in both Figure 2 and Figure 3. However, the overlap of the Willamette Valley and Coast Range populations in Figure 3 along the component 1 axis make it impossible to segregate these groups. The first two components account for 68.5 percent of the variation (Table 4). In Figure 3, the specimens from the Coast Range and the Willamette Valley are intimately intermixed, indicating that, based on the characters used in this PCA, the Willamette Valley and Coast Range populations of *S. nelsoniana* are not distinct morphologically. Similarly, the specimens from Walker Flat are closely intermixed with other Coast Range specimens, indicating that the population at Walker Flat is not a distinct taxon. The Coast Range populations are also not differentiated from the Willamette Valley populations

as 5-15 mm, rather than indicating that petal length in perfect flowers is 9-15 mm, while petal length in pistillate flowers is 5-9 mm. It is important to account for flower sex, as both perfect and pistillate-flowered plants are common. Examination of 32 populations of *S. nelsoniana* indicated the average ratio of pistillate-flowered plants to perfect-flowered plants is 1.36:1 (CH2M Hill 1987). Incorrect identification can result from using a key that fails to distinguish differences in petal and calyx size associated with flower sex. A key which allows for these differences, as well as utilizing other primary characteristics, is presented below:

TABLE 4. Eigenvectors for morphological parameters in each component of the principal component analysis of *Sidalcea nelsoniana*.

Parameter ¹	Component				
	1	2	3	4	5
BASTPU	-0.205	+0.535	+0.807	+0.141	+0.000
PETCOL	-0.000	+0.000	+0.000	+0.000	+1.000
CALCOL	-0.010	+0.830	-0.557	+0.026	+0.000
ADPETLG	+0.702	+0.016	+0.044	+0.710	+0.000
ADCALLG	+0.682	+0.157	+0.189	-0.689	+0.000
Variance					
Explained	43.1%	25.4%	24.2%	7.3%	0.0%

¹See Table 1 for definitions of parameters.

when the third and fourth components are examined (plots are not presented). These results agree with electrophoretic analysis of both leaf and seed proteins from Coast Range and Willamette Valley populations of *S. nelsoniana* (CH2M Hill 1986) which also show no differences among geographic populations of *S. nelsoniana*.

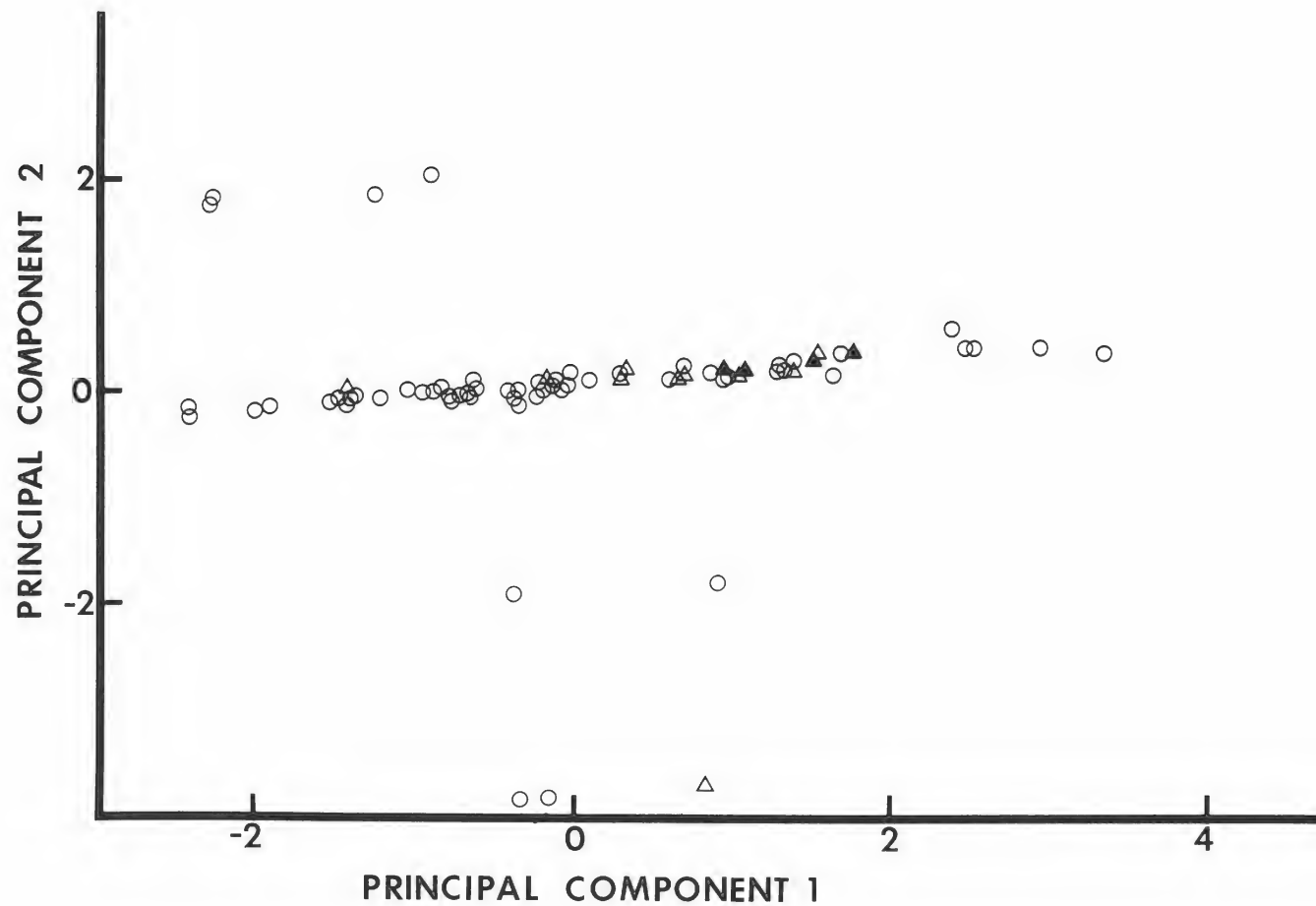


Figure 3. The first two principal components for specimens of *Sidalcea nelsoniana*, Willamette Valley (○), Coast Range (excluding Walker Flat) (△), and Walker Flat (▲).

An absolutely definitive statement on the genetic diversity between populations of *S. nelsoniana*, and in particular between those at Walker Flat and other locations, is beyond the scope of this study. However, to the extent that the taxonomic characteristics studied here are manifestations of the plants' genetic makeup, this study supports the hypothesis that the Walker Flat population is not genetically distinct from other populations, and that the loss of the Walker Flat population would not deplete the genetic diversity of the species.

In summary, analysis of pollen morphology and chromosome number, and the PCA of standard morphological traits have been used to confirm the species integrity of the four Willamette

Valley *Sidalcea*. Recent concerns over the taxonomic status of these species may have been influenced by oversight of the morphological variation within gynodioecious species. The analysis presented here also shows that *S. nelsoniana* is morphologically consistent throughout its range and so there is no basis for dividing the species into separate taxa.

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Impact of Grass Seedings on Establishment and Density of Diffuse Knapweed and Yellow Starthistle

Abstract

Knapweeds (*Centaurea* spp.) are major weed pests of northwestern rangelands, reducing productivity and accelerating erosion. Heavily infested rangelands need to be revegetated with forage species that can compete with knapweed, if they are to be returned to former levels of productivity. We conducted a two-year study to evaluate the survival of diffuse knapweed (*C. diffusa* Lam.) and yellow starthistle (*C. solstitialis* L.) during the establishment period of four rangeland grass species. 'Covar' sheep fescue (*Festuca ovina* L.) was the slowest grass to become established in the study. The biomass and early growth of 'Covar' controlled knapweed establishment during the second growing season. 'Ephraim' crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) provided an effective control of knapweed during the first growing season, but did not compete well with knapweed during the second growing season. 'Paiute' orchardgrass (*Dactylis glomerata* L.) and 'Critana' thickspike wheatgrass (*A. dasystachyum* (Hook.) Scribn.) controlled knapweed during both years of the study. The proximity of knapweed seeds to grass plants increased knapweed survival. These results indicate that the rate of reestablishment of knapweed on newly seeded range can be reduced by selecting grass species with competitive biomass and early growth characteristics.

Introduction

Diffuse knapweed (*Centaurea diffusa* Lam.) and yellow starthistle (*C. solstitialis* L.) are Eurasian plants that were introduced into the western United States and Canada at the turn of the century (Watson and Renney 1974, Roché and Talbott 1986). These weeds currently infest millions of acres of rangeland in the United States and Canada (Maddox 1979, Strang *et al.* 1979, Talbott 1987).

Domination of rangelands by knapweed result in substantial decreases in forage production (Watson and Renney 1974, Harris and Cranston 1979, Maddox 1979, Kelsey and Mihalovich 1987). The future productivity of these lands depends upon control of knapweed infestations and establishment of competitive forage plants. This study was designed to test the hypothesis that above- and below-ground phytomass of seeded grass species and knapweed seed placement would influence knapweed survival on newly seeded ranges.

Methods

A two-year study was conducted in northeastern Oregon (Union County). The area selected for the study produced 1350 kg/ha of diffuse knapweed in 1985. Precipitation amounts were 37.3 cm in 1986 and 26.0 cm in 1987 (Table 1). The site, a fine sandy loam, was mechanically treated by disking and planting 'Paiute' orchardgrass (*Dac-*

tylis glomerata L.), 'Ephraim' crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), 'Critana' thickspike wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.), and 'Covar' sheep fescue (*Festuca ovina* L.) in separate plots. The trial area (0.5 ha) was seeded (3-m drill box, 18-cm drill row spacing, 1 Pure Live Seed/linear cm) in March 1986 as a completely random design. Each species was replicated four times within the trial.

Grass phytomass was measured during June 1986 and 1987. Above- and below-ground phytomass was collected for each species using a 0.1-m² frame. The 20 cm x 50 cm frame, when centered on the drill row, extended to the center of the interspace. Above-ground phytomass was measured by clipping the plant material contained in the frame at ground level. Below-ground phytomass (crowns + roots) was measured by excavating the area contained in the frame to a depth of 25 cm, hand separating the root crown and roots over a screen, and handwashing the plant materials until it was free of foreign debris. Samples were oven dried (50°C) to a constant weight.

Reestablishment of diffuse knapweed from the soil seed bank in the grass stands was determined by counting knapweed density in 16 temporary transects in July 1986 and 1987. Each transect consisted of five 0.5-m² frames placed at random along a 10-m tape in the center of each drill strip (3-m x 25-m). Sampling avoided areas impacted by destructive sampling.

TABLE 1. Monthly precipitation amounts (cm) that occurred near the study area in 1986 and 1987.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1986	7.6	4.8	2.5	3.3	1.5	3.0	0.3	0.6	6.6	2.8	2.1	2.2
1987	3.8	3.0	2.3	2.1	4.0	4.5	1.0	0.0	0.0	0.0	2.8	2.5

Two *Centaurea* species were planted to ensure a known seed source on the site. Diffuse knapweed and yellow starthistle plots, containing 30 seeds in a 50-cm line, were planted separately in each drill strip. Placement of the plots was designed to establish two treatments per grass species (placement of the seeds within 3 cm of the root crown of the grass, and placement of the seeds in the center of the interspace between drill rows). Controls were established by planting seeds in tilled areas devoid of grass competition. All treatments were replicated four times. Planting occurred in October 1986, and *Centaurea* densities readings were recorded on May 15, June 15, and July 15 during the 1987 field season.

All data were evaluated using analysis of variance. Mean separations using least significant difference (LSD) tests are reported at a 0.05 level of significance, unless otherwise stated.

Results

Grass Response

Total phytomass (top, crown, root) in 1986 indicate 'Covar' was the slowest of the four species to establish during the seedling year (Table 2). 'Paiute' and 'Critana' were the dominant grasses, exceeding the phytomass of 'Covar' by 184 and 175 percent respectively. 'Ephraim' was the first species to emerge in 1986. However, 'Ephraim' yields were not significantly different from 'Covar' or the dominant grasses. Comparison of the above- and below-ground phytomass (crown + root) yielded similar results.

In 1987 'Paiute' and 'Covar' were the dominant grasses (Table 2). The above-ground phytomass of 'Covar' was greater than 'Paiute,' 'Critana,' and 'Ephraim.' Most of this difference can be attributed to the production of a large seed crop by 'Covar' in 1987. The below-ground phytomasses of 'Paiute' and 'Covar' were not significantly different from each other but were significantly greater than 'Ephraim' and 'Critana.'

TABLE 2. Phytomass (g/0.1-m²) of 'Critana' thickspike wheatgrass, 'Paiute' orchardgrass, 'Ephraim' crested wheatgrass, and 'Covar' sheep fescue in 1986 and 1987. Species means separated by letters are different (P = .05, n = 16).

	1986		
	Above-Ground Phytomass	Below-Ground Phytomass	Total Phytomass
'Critana'	13.0 a	12.2 a	25.2 a
'Paiute'	11.8 a	14.7 a	26.5 a
'Ephraim'	9.8 ab	11.1 ab	20.8 ab
'Covar'	7.2 b	7.2 b	14.4 b
LSD	3.2	4.85	7.28

	1987		
	Above-Ground Phytomass	Below-Ground Phytomass	Total Phytomass
'Critana'	21.5 b	32.1 b	53.1 b
'Paiute'	21.6 b	60.1 a	81.7 a
'Ephraim'	13.2 b	28.5 b	42.3 b
'Covar'	35.4 a	53.7 a	89.1 a
LSD	8.4	7.2	15.1

Diffuse Knapweed from the Soil Seed Bank

There was a significant difference between the number of knapweed seedlings associated with the different grasses in 1986 (Table 3). The 'Covar' seeding had more knapweed plants than 'Ephraim' or 'Paiute.' 'Critana' was not significantly different from 'Paiute,' 'Ephraim'

TABLE 3. Density (plants/m²) of diffuse knapweed in 'Critana' thickspike wheatgrass, 'Paiute' orchardgrass, 'Ephraim' crested wheatgrass, and 'Covar' sheep fescue seedlings. Species means separated by letters are different (P = .05, n = 80).

Grass species	Diffuse knapweed density	
	1986	1987
'Critana'	1.3 ab	0.4 a
'Paiute'	0.7 b	0.2 a
'Ephraim'	0.5 b	3.0 b
'Covar'	2.0 a	0.1 a
LSD	0.8	0.8

or 'Covar.' The 'Ephraim' and 'Paiute' seedlings emerged first and established vigorous stands during 1986, which is suggested here a primary reason for low knapweed establishment. During the second year (1987) 'Covar,' 'Paiute' and 'Critana' had significantly fewer knapweed seedlings than the 'Ephraim' seedlings (Table 3).

Centaurea Seed Plantings

Diffuse Knapweed. Diffuse knapweed seeds germinated in every plot (Table 4). The seedlings went through a natural thinning process as the growing season progressed. Seeds placed next to the crowns of the grasses had a slower rate of thinning than those planted in the center of the interspace between drill rows.

Grass species influenced diffuse knapweed survival when the seeds were planted next to the crown of the grass plant. By mid-July the control and 'Ephraim' treatments were the only plots containing knapweed seedlings (Table 4).

Yellow Starthistle. Survival of yellow starthistle seedlings mirrored that of diffuse knap-

weed except that a significant number of yellow starthistle seedlings survived in the 'Ephraim' stands in the center of the drill row as well as next to the grass plants (Table 5). Yellow starthistle plants that survived in grass stands beyond July 15 were dwarfed (10-12 cm tall) with a single flower contrasted with control plants that were 25-38 cm tall with multiple flowers.

These results support the reestablishment data for diffuse knapweed. 'Ephraim' is the most susceptible grass to establishment of diffuse knapweed and yellow starthistle seedlings during the second growing season. In addition, survivorship of diffuse knapweed and yellow starthistle seedlings in a grass stand was increased by placing seeds next to the grass crown.

Discussion

The survival of diffuse knapweed and yellow starthistle in a grass stand depends upon the ability of the grasses to occupy the site and use available resources. Knapweed survival responses in this study indicate that the rate and degree of

TABLE 4. Survival (percent of seeds planted) of diffuse knapweed in stands of 'Critana' thickspike wheatgrass, 'Paiute' orchardgrass, 'Ephraim' crested wheatgrass, and 'Covar' sheep fescue. Knapweed seeds were planted near the crown of the grass plants or in the interspace between drill rows. Means (percent survival and knapweed seedlings/50 cm) separated by letters are different ($P = .05$, $n = 20$).

	Crown Planting					
	May 15		June 15		July 15	
	Survival	Seedling Numbers	Survival	Seedling Numbers	Survival	Seedling Numbers
'Critana'	25.6%	7.7 a	12.3%	3.7 ab	0.0%	0.0 b
'Paiute'	9.0%	2.7 b	6.6%	2.0 b	0.0%	0.0 b
'Ephraim'	25.0%	7.5 a	19.0%	5.7 a	13.0%	4.0 a
'Covar'	20.0%	6.0 ab	11.6%	3.5 ab	0.0%	0.0 b
Control	16.6%	5.0 ab	18.0%	5.5 a	17.0%	5.2 a
LSD		4.4		2.6		1.2

	Interspace Planting					
	May 15		June 15		July 15	
	Survival	Seedling Numbers	Survival	Seedling Numbers	Survival	Seedling Numbers
'Critana'	11.6%	3.5 ab	<1.0%	0.2 b	0.0%	0.2 b
'Paiute'	0.0%	0.0 c	1.6%	0.5 b	0.0%	0.0 b
'Ephraim'	7.0%	2.2 abc	1.6%	0.5 b	2.3%	0.7 b
'Covar'	3.0%	1.0 bc	2.3%	0.7 b	1.6%	0.5 b
Control	16.6%	5.0 a	18.0%	5.5 a	17.0%	5.2 a
LSD		3.2		1.3		1.2

TABLE 5. Survival (percent of seeds planted) of yellow starthistle in stands of 'Critana' thickspike wheatgrass, 'Paiute' orchardgrass, 'Ephraim' crested wheatgrass, and 'Covar' sheep fescue. Starthistle seeds were planted near the crown of the grass plant or in the interspace between drill rows. Means (percent survival and starthistle seedling numbers/50 cm) separated by letters are different ($P = .05$, $n = 20$).

Crown Planting						
May 15		June 15		July 15		
Survival	Seedling Numbers	Survival	Seedling Numbers	Survival	Seedling Numbers	
'Critana'	9.0%	2.7 bc	6.0%	1.8 b	0.0%	0.0 c
'Paiute'	22.3%	6.7 abc	8.3%	2.5 ab	0.0%	0.0 c
'Ephraim'	26.6%	8.0 ab	15.6%	4.7 a	13.0%	4.0 a
'Covar'	12.3%	3.7 bc	8.3%	2.5 ab	5.6%	1.7 b
Control	33.0%	10.0 a	16.6%	5.0 a	13.0%	4.0 a
LSD		4.6		2.5		1.1

Interspace Planting						
May 15		June 15		July 15		
Survival	Seedling Numbers	Survival	Seedling Numbers	Survival	Seedling Numbers	
'Critana'	11.6%	3.5 b	<1.0%	0.2 b	0.0%	0.0 c
'Paiute'	0.0%	0.0 b	1.6%	0.5 b	<1.0%	0.1 c
'Ephraim'	11.6%	3.5 b	5.0%	1.5 b	5.0%	1.5 b
'Covar'	<1.0%	0.2 b	5.0%	1.5 b	2.3%	0.7 bc
Control	33.0%	10.0 a	16.6%	5.0 a	13.0%	4.0 a
LSD		3.6		1.3		1.1

site occupation is different for each of the grass species.

'Covar' sheep fescue was the slowest of the four grass species to establish. The performance of 'Covar' was similar to that described by Hafenrichter *et al.* (1968) and Tiedemann and Klock (1974) for 'Durar' hard fescue (*F. ovina* L.). 'Covar' seedlings had a significant number of diffuse knapweed seedlings (2 knapweed/m²; Table 3) during the first year of grass establishment. However, 'Covar' demonstrated a strong second year growth response which allowed it to dominate the site. Consequently, the establishment of new knapweed plants during the second growing season was minimal.

'Ephraim' crested wheatgrass demonstrated a high seedling and first year vigor which resulted in a low knapweed density. The second year growth rate of 'Ephraim' was the lowest observed for any of the grasses studied. Knapweed establishment during the second growing season was significantly higher (3 knapweed/m²) than any of the other grass species.

'Paiute' orchardgrass was one of the most productive grasses in both years of the study. As a result, 'Paiute' orchardgrass was relatively free of knapweed seedlings during both growing seasons.

'Critana' thickspike wheatgrass was a dominant grass during the first year of establishment but had a second year growth rate that leveled out at a lower total phytomass than either 'Paiute' or 'Covar.' 'Critana' was relatively knapweed-free during the first year of establishment and although it had more knapweed seedlings in the second year of growth the number of seedlings was not significantly different from those found in 'Covar' or 'Paiute' seedlings.

Centaurea seedling survival was influenced by seed placement. Seedling survival was longest in the microclimate next to the grass crowns. Survival of both knapweed species next to a grass plant appears to be directly influenced by the amount of grass phytomass. 'Ephraim' crested wheatgrass which had the lowest total phytomass during the second growing season was most

susceptible to knapweed establishment. This relationship is also influenced by the amount of overlap between the active growth periods of the grass and the species of knapweed. For example, knapweed seeds planted next to 'Covar' root crowns had a higher rate of establishment than those planted next to 'Critana' or 'Paiute.' This difference may be because 'Covar' completed its annual life cycle prior to periods of moisture stress. Consequently, the stress placed on knapweed seedlings by 'Covar' was not as great as the stress placed on the knapweed seedlings next to 'Paiute' and 'Critana' plants which were actively growing during periods of moisture stress.

Data from this study do not imply that a grass species will totally prevent knapweed establishment in an area where there is a seed source.

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- Similar results were reported by Huston *et al.* (1984) where a treatment of picloram and intermediate wheatgrass (*A. intermedium* (Host) Beauv.) reduced, but did not eliminate starthistle from study plots. A critical element in both studies appears to be the establishment of a grass species that will remove a significant proportion of the moisture and nutrients from the rooting zone of knapweed seedlings and overlap the active growth period of the knapweed species. In addition both studies used techniques that reduced initial knapweed competition. In the Huston study picloram was used to inhibit knapweed competition, whereas this study used tillage of the seedbed to bury a portion of the knapweed seed bank. We believe an initial control of knapweed competition is essential for quick establishment of new grass seedings.

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A Small Mammal Fauna from the Touchet Beds of Walla Walla County, Washington: Support for the Multiple-Flood Hypothesis

Abstract

Recent work in southeastern Washington has challenged the long-accepted hypothesis that the late Pleistocene Touchet Beds were deposited by one or a few colossal glacial outburst floods from glacial Lake Missoula in western Montana. Work conducted for this study in the northern portion of the Walla Walla Valley has revealed the presence of a diverse and exceedingly well-preserved small-mammal fauna from the middle portion of these flood-related sediments. The remains are preserved with fragile bone elements and dentition intact and virtually no evidence for post-mortem transport or reworking. Biogenic structures interpreted as rodent burrows are prevalent throughout the section. Sedimentary structures and textures preserved at the fossil collection site suggest that the sediments were deposited under conditions of considerable turbulence, and that there were periods of time between depositional episodes characterized by erosion and colonization by small mammals. The data are overwhelmingly supportive of a hypothesis which invokes multiple flood episodes separated in time by decades-long periods of exposure for deposition of the Touchet Beds.

Introduction

The Touchet Beds (late Pleistocene) are widespread in the Walla Walla Valley of southeastern Washington (Figure 1), mantling the

Miocene Columbia River Basalt Group and covering the Pliocene and earlier Pleistocene valley fill deposits. The Touchet Beds and associated erosional topography of the Channeled Scablands

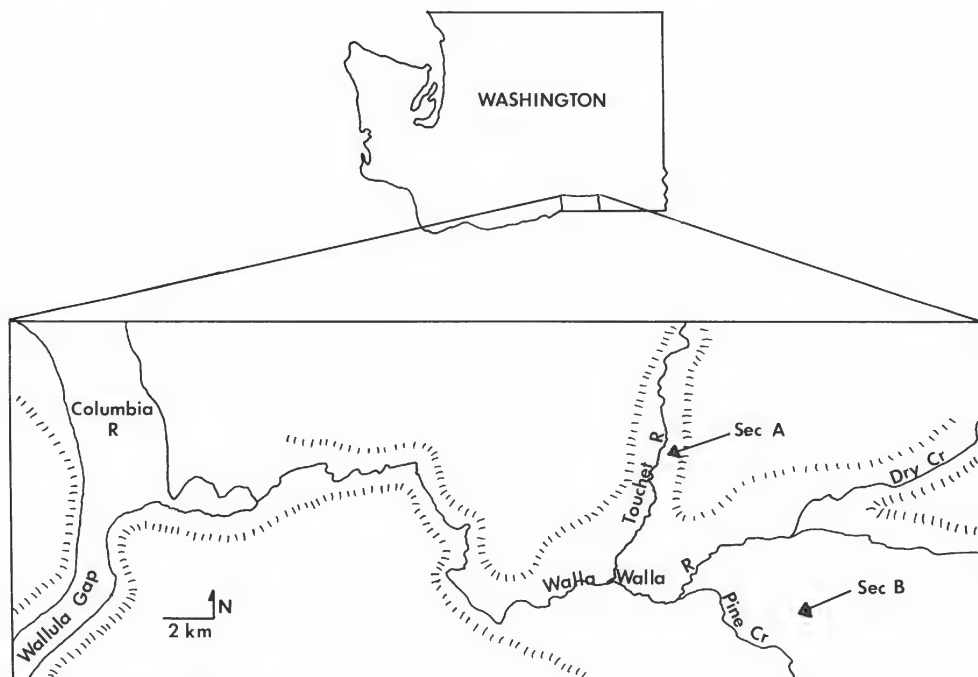


Figure 1. Index map of the Walla Walla Valley showing approximate limits of distribution of the Late Pleistocene Touchet Beds (hatch marks), and location of study sections. Section A represents the Touchet River section, section B the Burlingame Canyon section. After Bjornstad (1980).

have long been recognized as having resulted from flood waters released from the ice-dammed glacial Lake Missoula in western Montana. Exposures of the Touchet Beds in the Pasco Basin and Walla Walla Valley of southeastern Washington comprise a distinctive sequence of graded rhythmites laid down as water backed up behind a hydraulic dam at Wallula Gap, the only outlet for water entering the region (Figure 1).

The mechanisms responsible for deposition of the Touchet Beds have been argued for some time, and from this argument, two schools of thought have emerged. The first interprets the Touchet Beds as the result of a single massive flood or a few floods, with hydraulic surging of the floodwaters giving rise to the characteristic graded rhythmites (Bretz 1923, 1925, 1930, 1969; Bretz *et al.* 1956; Baker 1978; Carson *et al.* 1978; Waitt, 1978; Bjornstadt 1980). The second considers the Touchet Beds as having been deposited by as many as forty or more separate floods, each giving rise to a graded rhythmite, separated in time by decades-long periods of exposure. This view of the Touchet Beds was pioneered by Waitt (1980, 1984, 1985a, 1985b), and supported by Atwater (1984).

This paper will examine the vertebrate fauna and associated biogenic structures recovered from an exposure of the Touchet Beds in the northern Walla Walla Valley. In addition, the sedimentologic characteristics observed at the outcrop will be discussed and interpreted in light of the prevailing ideas regarding depositional mode of the Touchet Beds.

Vertebrate Fauna

Vertebrate fossils belonging to the Order Rodentia have been recovered from the Touchet River section (section A, Figure 1). Represented in the collection to date are members of the families Sciuridae (ground squirrel, 2 skulls), Cricetidae (vole, 1 skull), Heteromyidae (kangaroo rat, partial skull), and post-cranial remains of at least four other individuals from the Order Rodentia. Species-level taxonomy with such a paucity of material is unproductive; however, preliminary study of the fossils shows them to be indistinguishable from species which now inhabit the region.

One of the sciurid skulls in particular is worthy of special consideration because of its

unusually good preservation (Figure 2). This specimen was recovered from a clastic dike approximately 1 m below a thin tephra layer. Bjornstadt (1980) analyzed a tephra at a nearby locality, which occurred at the same apparent stratigraphic level and exhibited similar structures. He found this tephra to fall within the Mt. St. Helens set 'S' chemical group. The Mt. St. Helens set 'S' tephra has been dated at approximately 13,000 ybp (Mullineaux and Crandell 1981). The dike appears to originate from below the collection locality, and thus the skull most likely predates the tephra, which is here approximately 3 m below the modern topographic surface. The base of the Touchet Beds is not exposed in the Walla Walla Valley. At Burlingame Canyon (section B, Figure 1) the section extends for tens of meters below the St. Helens set 'S' tephra. It is, thus, likely that the original depositional locality for the skull is above the base of the Touchet Beds and below the St. Helens 'S' tephra.

Of particular interest is the state of preservation of the skull. All of the dentition is intact (Figure 3a). The zygomatic arches, likewise, are preserved without damage (Figure 3a). The auditory bullae, which are delicate features on recent skull material, are intact (Figure 3b) and the pterygoid processes (Figure 3b) are preserved with minimal damage. Finally, the skull exhibits virtually no evidence for abrasion as a result of post-mortem transport. Other cranial elements are not intact, but had disintegrated in outcrop. Post-cranial remains exhibit excellent preservation, with no evidence for abrasion.

If the Touchet Beds were the result of a single flood, or few floods characterized by hydraulic surging, then the presence of well-preserved, unabraded mammalian remains from the middle portion of the deposit is problematical. If the remains represent members of the local fauna entombed by the initial flood surge, they might be preserved in their present condition, but at or near the base of the deposit. If the remains were transported into the area by a later flood surge, they might be preserved in the middle of the deposit, but would certainly exhibit evidence of transport, such as abraded surfaces and/or broken features. The best explanation for the occurrence of a well-preserved mammalian fauna in the middle of the Touchet Beds is that it represents the remains of an established local fauna which experienced minimal (or no)



Figure 2. Sciurid skull recovered from a clastic dike in the Touchet River section of the Touchet Beds. A: dorsal view; B: ventral view; C: left lateral oblique view.



Figure 3. A: Upper left dentition and zygomatic arch of sciurid (ground squirrel) skull. B: Auditory bullae (1) and pterygoid process (2) of sciurid skull. Specimen from Touchet River section. Scale bar equals 0.5 cm.

transport during a distinct flood episode. This is consistent with other physical and biogenic evidence presented in the following section and is supportive of the hypothesis which invokes multiple flood episodes with decades-long exposure between floods.

Sedimentology

Two well-exposed sections of Touchet Beds were sampled for this study (see location map, Figure 1). Stratigraphic control within the sections is provided by the occurrence of Mt. St. Helens set 'S' tephra at the top of each sampled interval. The Burlingame Canyon section (section B, Figure 1) represents what is considered to be typical of the Touchet Beds in this region. The Touchet River section (section A, Figure 1), from which the fossils were recovered, represents somewhat different sedimentologic conditions as interpreted from differences in grain size parameters, physical sedimentary structures, and geographic location.

The Burlingame Canyon section, where there are as many as 40 rhythmites exposed, displays well-developed graded bedding within each rhythmite, with the basal sand giving way upward to silt representing standing water, and in some cases, a thin veneer of massive silt capping the rhythmite. Mean grain size for samples representing the base, middle, and top of rhythmites reflects this fining-upward trend (Figure 4, lower right). Values for standard deviation (a measure of sorting) show corresponding variation within each rhythmite (Figure 4, upper right). Samples from the Touchet River section do not show the same trends in grain size distribution. Mean grain sizes generally show low or erratic variability within rhythmites as well as consistently smaller mean grain size (Figure 4, lower left). Similarly, sorting values are considerably more consistent, again with little apparent trend within rhythmites (Figure 4, upper left). In addition, rhythmites from the Touchet River section do not have clear upper and lower boundaries and were difficult to distinguish visually while in the field.

Plots of standard deviation (sorting) versus mean grain size are shown in Figure 5. Samples from the Burlingame Canyon section (Figure 5, right) allow reasonable grouping of data points into lower, middle, and upper rhythmites. The Touchet River section (Figure 5, left), by contrast,

shows relatively tight grouping of all data points, and poor separation of lower, middle, and upper rhythmites. The graphic data supports the field observation that rhythmites are poorly developed in the Touchet River section as compared to the Burlingame Canyon section.

Sedimentary Structures: Primary sedimentary structures observable in outcrops can be used to interpret the conditions of deposition in the two study sections. The Burlingame Canyon section shows, from base to top within each rhythmite, a transition from planar bedding (lower-upper flow regime transition) to ripples and climbing ripples, and finally to massive bedding reflecting deposition from suspension and/or eolian deposition. These structures suggest an initial flood surge and deposition of a traction load followed by rapidly decreasing energy. In addition, paleocurrent directions are consistently up-valley for the lower to middle portions of rhythmites. The Touchet River section, while displaying moderately well-developed ripples and cross-stratification, shows no clearly definable transition in flood energy within rhythmites. Planar beds were not noted, and massive bedding at the tops of rhythmites was irregularly preserved. In addition, ripples did not show a consistent orientation, suggesting that paleocurrent directions were highly variable.

Biogenic sedimentary structures, primarily small-diameter cylindrical features attributed by Waitt (1980) to burrowing activity of rodents, are prevalent throughout both sample sections. Alcorn (1940) has indicated that modern rodents burrow to a maximum depth of 2 m below ground surface. The presence of burrows throughout thick sections of the Touchet Beds suggests that they are a result of burrowing which was contemporaneous with deposition, rather than a result of the burrowing activity of modern rodents. In addition, Waitt (1980) pointed out that the burrow-filling sediment is compacted to a degree equivalent to that of the surrounding sediment, suggesting contemporaneous compaction of the Touchet Beds and the burrow-filling sediment. The St. Helens set 'S' tephra is extensively perforated by small diameter (less than 1 cm) features, which Spencer (1987) suggested might be insect burrows and which may indicate exposure or near exposure subsequent to deposition of the tephra. An alternative explanation for these features was presented by Bjornstadt (1980):

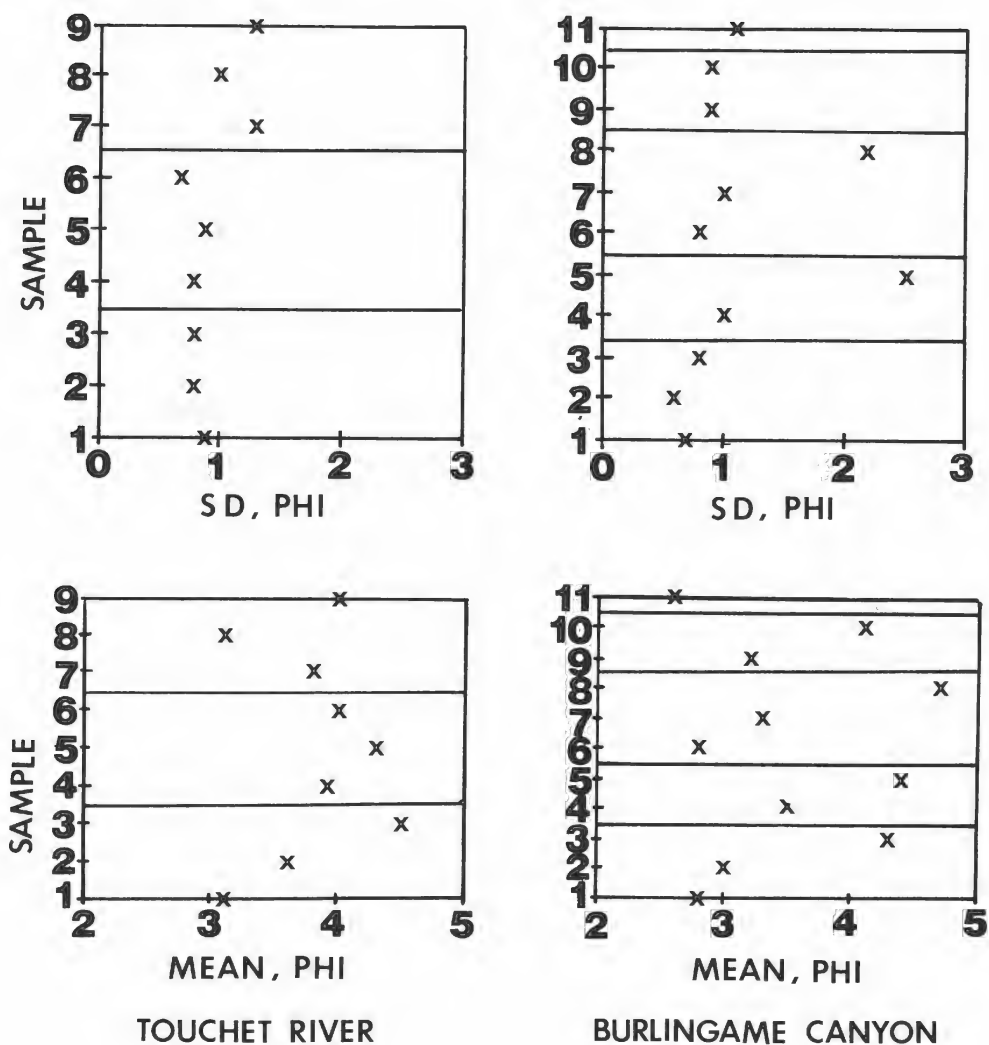


Figure 4. Plots of Standard Deviation versus sample (upper graphs) and Mean grain size versus sample (lower graphs) for the Touchet River section (left) and the Burlingame Canyon section (right). Solid horizontal lines represent rhythmite boundaries. Mount St. Helens set 'S' tephra located at top of each sampled interval.

he proposed that they represent hydroplastic injection structures.

The tephra itself may be used to suggest exposure or near exposure at the time of its deposition. It is difficult to envision an airfall tephra accumulating to a thickness of a few centimeters if the valley was occupied by deep, turbulent waters resulting from a single flood. The thick-

ness and purity of the tephra suggests a valley which was drained or nearly drained at the time of deposition.

The sedimentologic data is best explained as a result of the size and location of tributary valleys (Touchet River section) with respect to the Walla Walla Valley (Burlingame Canyon section). The center of the Walla Walla Valley (section B,

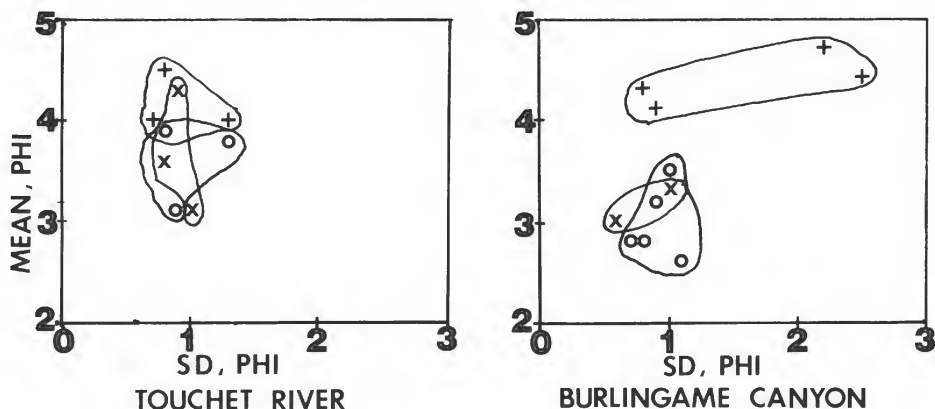


Figure 5. Plots of Standard Deviation versus Mean grain size for the Touchet River section (left) and the Burlingame Canyon section (right). Samples grouped according to position within rhythmite (+: upper; x: middle; o: lower).

Figure 1) would be expected to experience the most variability in conditions during advancing floods. In these areas, sedimentary structures and statistical parameters of sediments reflect rapidly changing energy conditions during flooding. Tributary valleys (Touchet River section, section A, Figure 1) would be expected to be more continuously turbulent (conditions more uniform) as a result of the fact that they are both shallower and narrower than the main valley. In addition, the higher elevation tributary valleys would be the first to drain after a flood episode, and would experience more intense post-flood erosion, and thus removal of upper rhythmites, as a result of their higher gradient. Observed structures and statistical parameters for the Touchet River section reflect these phenomena.

Conclusions

Small-mammal fossils recovered from an exposure of the late Pleistocene Touchet Beds are exceedingly well-preserved, with fragile bone elements and dentition preserved unbroken. In addition, the fossils show no evidence for abrasion or reworking, suggesting little or no transport prior to burial and fossilization. Associated with the fossils, and present throughout both study sections, are abundant rodent burrows. The available evidence indicates that the fossils represent the remains of members of an established local community of mammals

which was destroyed during a distinct flood episode.

Sedimentologic parameters for samples from two measured sections of the Touchet Beds suggest that the conditions of deposition of these sediments were variable dependent upon geographic location within the Walla Walla Valley region. The Burlingame Canyon section, located in the center of the Walla Walla Valley, was characterized by rapidly decreasing energy during flood episodes, which resulted in well-developed graded rhythmites. The Touchet River section, located in a narrower, shallower tributary valley, was characterized by uniformly turbulent conditions during deposition, which resulted in poorly-developed graded rhythmites. In addition, the higher elevation and steeper gradient of the tributary valley gave rise to more rapid drainage, and more vigorous post-flood erosion. This, in turn, resulted in removal of the fine-grained upper portion of the rhythmites in the Touchet River section.

The presence of a well-preserved small-mammal fauna within these sediments strongly supports the hypothesis which invokes multiple flood episodes, separated by decades-long periods of exposure characterized by erosion and/or non-deposition, to explain the deposition of the Touchet Beds.

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Habitat Features and Trout Abundance Relative to Gradient in Some Wyoming Streams

Abstract

Channel gradient has been shown to have a negative relation to trout standing stocks indicating that separation of stream channels into gradient classes may provide a better understanding of the relationships between habitat and trout abundance. Our major objective was to determine if there are significant differences in habitat features and standing stocks of trout > 100 mm between two classes of channel gradient, low (0.1-1.4% channel slope) and moderate (1.5-4.0%). We also determined statistical relations between habitat features and trout standing stocks in each class of channel for unaltered streams on the Medicine Bow National Forest, Wyoming. Low-gradient reaches were found to have deeper nearshore water depths, more undercut banks, and more trench pools than moderate-gradient reaches, while moderate-gradient reaches had more cobble substrate, dammed pools formed by woody debris, and plunge pools. The mean standing stock was 267 kg/ha in low-gradient reaches and 102 kg/ha in moderate-gradient reaches. Habitat features correlated with trout standing stocks differed between the two gradient classes. Our results demonstrate that separation of stream segments into reaches of similar gradient are important in identifying features of trout habitat that are otherwise obscured by variation over a wider gradient range.

Introduction

Various investigators have found the gradient of stream channels to be negatively correlated with the abundance of brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* (Kennedy and Strange 1982, Hermansen and Krog 1984, Chisholm and Hubert 1986, Fausch in press). The results suggested that habitat features and structural elements were different among channels of differing gradients. In other studies Reeves and Everest (1986) used a channel-typing system (Rosgen 1985) in western Oregon coastal streams and found differences in microhabitat and salmonid abundance between channels of different gradients. We felt that the separation of stream channels by gradient could provide a better means to understand the factors influencing trout abundance and to predict brook trout and brown trout standing stocks in Rocky Mountain streams. Our main objective was to determine if there are significant differences in habitat features and standing stock of trout > 100 mm total length between two classes of channel gradient, low (0.1-1.4% channel slope) and moderate (1.5-4.0%). We also determined statistical relations

between habitat features and trout standing stocks in each class of channel.

Study Area

All study streams were in Medicine Bow National Forest (MBNF), south of Wyoming Highway 130 on the Snowy Range and east of the Continental Divide on the Sierra Madre. No native salmonids were in the study area, but brook trout and brown trout have been introduced. Populations are maintained by natural reproduction. Only brook trout inhabit the streams at elevations of > 2,450 m. At lower elevations reaches are inhabited by both brook trout and brown trout, while others have only brown trout.

Potential study streams extended from 2350 to 3000 m above mean sea level within the North Platte River drainage in MBNF. About 8 percent of all stream channels in the study area have a low gradient (0.1-1.4% channel slope) and 90 percent have a moderate gradient (1.5-4.0%). We selected 15 watersheds that had been minimally affected by human activity with no history of clearcut logging, overgrazing, or mining. Potential study reaches were selected from U.S. Forest Service records and U.S. Geologic Survey topographic maps. Low-gradient and moderate-gradient reaches at least 200 m in length were marked on the maps. Specific sampling sites were

¹The Unit is jointly supported by the University of Wyoming, the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service.

selected to represent the range of drainage basin areas (0.7-100 km²) and elevations occurring in the study area. Selected study reaches and the upstream watershed area were ground truthed to confirm the lack of human effects. Channel gradients were assessed with a surveyor's level prior to field sampling.

A total of 16 low-gradient reaches and 32 moderate-gradient reaches were selected for study. The 16 low-gradient reaches were classified as C3 channels using Rosgen's (1985) channel classification system, while the moderate-gradient reaches were classified as B2 and B3 with 16 reaches in each class. Low-gradient reaches ranged from 2420 to 2975 m above mean sea level and tended to be in either headwater or foothill regions. The wetted widths during late summer ranged from 0.4 to 6.8 m (drainage basin area range = 0.7-95.0 km²). Moderate-gradient reaches ranged from 2377 to 2963 m in elevation and had wetted widths of 1.1 to 9.3 m (drainage basin area range = 2.2-96.2 km²).

The underlying geology and the riparian zone contributed to differences between the two gradient classes. The low-gradient channels were almost exclusively in meadow areas with alluvial soils where large trees were lacking, but dense growths of willows, sedges, and grasses allowed overhanging banks to form as meander processes occurred. Subsequently, low-gradient channels tended to have undercut banks and trench pools with accumulation of fine sediment substrate that could support aquatic vegetation, but woody debris was generally lacking. In contrast, moderate-gradient channels were almost exclusively in coniferous forest, where large trees were present at or near the water's edge, with geologic formations preventing meander processes from having a pronounced effect. So moderate-gradient channels tended to have more dammed pools and plunge pools formed by geologic formations and woody debris, coarser substrates with less fine sediment, more riffle habitat, limited amounts of undercut bank and trench pools, and less aquatic vegetation than low-gradient channels.

Methods

We used the transect method to measure stream habitat features over 200-m reaches (Platts *et al.* 1983). Riffles marked the upper and lower ends of study reaches. In 1985 we spaced transects 2 m

apart and made point measurements at 0.3-m intervals; in 1986 the intervals were 4 m apart and the point measurements were made at seven equally spaced locations not including the banks.

Water-depths were measured at each point; shore-depth measurements were excluded from calculations of mean depth. At each point interval across a transect, we visually classified cover, dominant substrate, embeddedness, and micro-habitat. Cover was classified into three categories: aquatic vegetation, woody debris, or boulder. Substrate was classified into six categories (after Platts *et al.* 1983; diameter in parentheses): small fine sediment (diameter $\leq$ 0.8 mm), large fine sediment (0.9-4.7 mm), gravel (4.8-76.0 mm), cobble (77-304 mm), small boulder (305-609 mm), and large boulder ($\geq$ 610 mm). Embeddedness (amount of fine sediment surrounding the underlying substrate particles) was rated from zero to 100% (Platts *et al.* 1983). We classified habitat types according to Bisson *et al.* (1982). Shore depth, undercut bank, and overhanging vegetation were measured at each bank with a measuring staff. Bank angle was determined with a clinometer (Platts *et al.* 1983).

We measured the length of each pool and riffle and noted the physical structure associated with the formation of the pool—such as geologic formations (bedrock, boulders) or woody debris (log check dams, natural log deflectors, and debris jams). We also computed the percentages of pool habitat created by geologic controls and woody debris; most woody debris probably overlaid geologic formations, but where it was the evident feature governing pool formation, the location was identified.

We used the removal method of DeLury (1951) to estimate trout standing stock over the study reaches during late summer and early autumn while the streams were at base flow. Each reach was blocked at the upper and lower end with small-mesh seines to prevent upstream or downstream movement of trout. Three depletion passes were made with a Coffelt Model BP-2 backpack electroshocker. Fish from each pass were individually weighed to the nearest gram and measured (total length) to the nearest millimeter. Only fish longer than 100 mm were used in population estimates. We used program CAPTURE of White *et al.* (1982) to estimate trout populations, choosing model M(bh) because it allowed for variability in behavioral responses of fish to the first capture attempt.

We used Scheffe's test for comparison of means between low-gradient and moderate-gradient reaches (Zar 1984). An arcsine transformation was performed on all proportional data, but means of measured values were reported. Pearson product-moment correlation analyses were performed to determine univariate relations between stream habitat features and standing stocks of trout. Stepwise discriminant function analyses were performed to identify the major differences in habitat features between low-gradient and moderate-gradient channels (Nie *et al.* 1975). The univariate comparisons of means provided insight into habitat differences, but the results were confounded by the lack of independence among the variables. Discriminant function analysis was used to eliminate the confounding effect of intercorrelation among habitat variables. Stepwise multiple-regression analyses were used to develop models that accounted for variation in trout standing stock using variables identified as important in the discriminant function analyses (Nie *et al.* 1975). All statistical differences were accepted as significant at $P \leq 0.05$.

Results

Habitat Differences

Twenty-nine habitat variables were analyzed to determine if they differed in abundance between low-gradient and moderate-gradient channels (Table 1). The habitat variables were separated into four groups—channel morphology, cover, substrate and habitat type—based on the channel features they described.

Four of the six channel-morphology variables were significantly different between the low-gradient and moderate-gradient channels that we studied (Table 1). The low-gradient channels were deeper and narrower, a larger proportion of the bank adjoined deep water, and the banks tended to have more overhang than the moderate-gradient channels. The best discriminant function to describe differences in habitat features between low-gradient and moderate-gradient channels used two variables, mean shore depth and the percentage of bank with a bank angle $< 45^\circ$. This discriminant function properly classified 39 of 48 study reaches.

Of the eight cover features measured, three were significantly different between the two channel types (Table 1). Both undercut banks and

aquatic vegetation were more abundant in low-gradient reaches than in moderate-gradient reaches. Woody debris formed an average of only 4 percent of the pool habitat (includes all pool types) in low-gradient reaches, but 24 percent in moderate-gradient reaches. Discriminant function analysis identified three cover variables as the best to distinguish between the two channel types—percentage of undercut bank, pool habitat 30 cm deep, and woody debris forming pool habitat. This discriminant function correctly classified 43 of 48 study reaches.

As would be expected, substrate features differed between the two gradient classes (Table 1). The abundance of large and small sediment was greater in low-gradient channels, as well as embeddedness, while cobble was more abundant in moderate-gradient channels. Only one substrate variable, cobble, was identified in the discriminant analysis and this variable correctly classified 41 of 48 study reaches.

The abundance of four habitat types differed significantly between the two classes of channel gradients (Table 1). Low-gradient reaches tended to have more trench pools, but fewer riffles, plunge pools, and dammed pools than in moderate-gradient reaches. The best discriminant function to describe habitat differences between the two gradient classes included trench pools, secondary channel pools, and plunge pools. This discriminant function properly classified 45 of 48 study reaches.

Trout Standing Stocks

The mean standing stock of trout differed significantly between low-gradient and moderate-gradient reaches. The mean in low-gradient reaches was 267 kg/ha (SD = 175, range = 50-611) and in moderate-gradient reaches was 102 kg/ha (SD = 49, range = 36-204).

Brook trout and brown trout standing stocks in low-gradient and in moderate-gradient reaches were evaluated separately where allopatric and sympatric populations occurred (Table 2). Among allopatric populations, mean brook trout standing stocks were more than twice as great in low-gradient than in moderate-gradient; however, mean brown trout standing stocks were similar, but the sample sizes were small with only 3 and 4 reaches in each category. Among sympatric populations of brook trout and brown trout,

TABLE 1. Means for channel morphology, stream cover, substrate, and habitat variables measured in low-gradient (0.1-1.4%) and moderate-gradient (1.5-4.0%) stream reaches on the Medicine Bow National Forest, Wyoming. Asterisk indicates a significant difference using Scheffe's test ($P \leq 0.05$).

Variable	Channel gradient (%)			
	0.1-1.4		1.5-4.0	
	Mean	Range	Mean	Range
Channel morphology				
Water depth (cm)*	19.7	10.9-33.8	14.6	8.3-23.8
Bank angle < 90° (%)*	53.5	24.4-90.2	29.0	9.2-63.8
Bank angle < 45° (%)*	20.2	8.0-31.4	12.7	2.6-25.4
Width-to-depth ratio	7.0	2.0-23.5	10.6	2.5-22.1
Shore depth (cm)	12.8	8.4-19.6	7.8	5.2-12.7
Shore depth $\geq$ 15.2 cm (%)	36.8	18.2-66.3	16.8	5.5-63.3
Cover				
Undercut bank (%)*	53.0	24.4-90.2	26.0	7.9-63.8
Overhanging vegetation (%)	44.1	9.9-77.9	29.7	4.0-75.9
Boulder cover (%)	0.2	0.0- 1.0	0.9	0.0- 6.6
Woody cover (%)	3.2	0.0-13.9	4.5	0.0-11.6
Aquatic vegetation cover (%)*	11.5	0.0-62.7	3.8	0.0-34.7
Pool $\geq$ 30.5 cm deep (%)	34.4	0.0-87.3	20.6	0.0-51.8
Pools with cover (%)	13.9	0.0-55.4	12.8	0.0-28.6
Woody debris control (%)*	4.0	0.0-40.0	24.5	0.0-54.4
Substrate				
Large boulder (%)	0.9	0.0-11.5	4.0	0.0-27.5
Small boulder (%)	4.9	0.0-28.6	11.6	0.6-27.1
Cobble (%)*	21.4	2.6-44.9	40.3	24.1-67.6
Gravel (%)	47.0	7.6-77.4	36.0	10.8-67.9
Large fine sediment (%)*	12.8	0.3-36.7	2.4	0.0- 8.8
Small fine sediment (%)*	13.0	0.0-53.1	1.0	0.0- 6.2
Embeddedness (%)*	58.7	26.9-97.5	21.4	14.7-61.4
Habitat type				
Riffle (%)*	25.4	7.7-54.8	39.9	13.9-61.6
Rapid (%)	0.2	0.0- 2.1	1.9	0.0-10.7
Secondary channel pool (%)	0.3	0.0- 1.5	0.9	0.0- 4.9
Backwater pool (%)	8.2	0.0-20.9	14.4	2.8-27.2
Trench pool (%)*	30.3	7.7-67.0	5.2	0.0-20.8
Plunge pool (%)*	0.5	0.0- 2.9	4.0	0.0-17.3
Dammed pool	1.5	0.0-11.3	5.2	0.0-22.1
Glide (%)	31.6	18.2-45.1	27.4	11.1-58.6

brook trout standing stocks were about three times greater in low-gradient channels and standing stocks of both species together averaged almost four times greater in low-gradient reaches.

The habitat features that were correlated with trout abundance differed between low-gradient

and moderate-gradient reaches (Table 3). Total standing stock increased with increasing amounts of deep nearshore area, undercut bank, overhanging vegetation, trench pools, and plunge pools, but decreased with increasing water depth, width-to-depth ratio, and riffle abundance among the

TABLE 2. Mean standing stocks (kg/ha) of allopatric and sympatric population of brook trout and brown trout in low-gradient and moderate-gradient stream reaches on the Medicine Bow National Forest, Wyoming.

		Allopatric		Sympatric		
		Brook trout	Brown trout	Brook trout	Brown trout	Both trout
Low	Mean	283	61	224	128	352
	SD	103	8	175	34	190
	n	7	3	6	6	6
Moderate	Mean	131	57	43	42	85
	SD	42	16	33	23	28
	N	14	4	14	14	14

low-gradient reaches. In the moderate-gradient reaches, standing stock was positively correlated with deep nearshore area, overhanging vegetation, aquatic vegetation, fine sediment, embeddedness, and glide habitat, but negatively correlated with width-to-depth ratio, deep pools, boulder and cobble substrate, and backwater pools. A few variables were correlated with trout abundance in both gradient classes; deep nearshore areas and overhanging vegetation were positively correlated, while width-to-depth ratio was negatively correlated.

Brook trout standing stocks were found to be correlated with only one habitat feature among low-gradient reaches (Table 3); as width-to-depth ratio increased brook trout abundance declined.

TABLE 3. Statistically significant ($P \leq 0.05$) correlation coefficients for relations between trout standing stock and measured habitat features in low-gradient and moderate-gradient reaches on the Medicine Bow National Forest, Wyoming.

Variable	Channel gradient (%)					
	1.0-1.4			1.5-4.0		
	Total trout (n = 16)	Brook trout (n = 13)	Brown trout (n = 9)	Total trout (n = 32)	Brook trout (n = 28)	Brown trout (n = 18)
Channel morphology						
Water depth (cm)	—0.57		—0.89			0.47
Width-to-depth ratio	—0.61	—0.75		—0.37	—0.52	
Bank angle < 90° (%)	0.60					—0.40
Shore Depth ≥ 15.2 cm (%)	0.44			0.38	0.37	
Cover						
Undercut bank (%)	0.60					
Overhanging vegetation (%)	0.48			0.40	0.54	
Aquatic vegetation cover (%)			0.75	0.44	0.45	
Pool habitat ≥ 30.5 cm deep (%)			—0.89	—0.40	—0.41	
Pools with cover (%)			0.65			—0.47
Substrate						
Small boulder (%)			0.60	—0.34		
Cobble (%)				—0.30		
Large fine sediment (%)				0.50	0.39	
Small fine sediment (%)				0.48	0.44	
Embeddedness (%)				0.51	0.39	
Riffle (%)	—0.44					
Backwater pool (%)			0.72	—0.31		
Trench pool (%)		0.48	0.61			
Plunge pool (%)		0.45	0.62			
Glide (%)				0.46	0.47	—0.45

Several habitat features were correlated with brook trout abundance in moderate-gradient reaches. In moderate-gradient reaches brook trout abundance increased with greater proportions of shore depth ≥ 15.2 cm deep, overhanging vegetation, aquatic vegetation, aquatic vegetation cover, large and fine sediment, embeddedness, and glide habitat. Brook trout abundance went down as width-to-depth ratio increased and the abundance of pool habitat ≥ 30.5 cm deep increased.

The habitat features correlated brown trout standing stocks differed from those related to brook trout abundance. Among low gradient reaches, brown trout standing stocks increased with greater proportions of aquatic vegetation cover, pools with cover, boulder cover, backwater pools, trench pools, and plunge pools. Within low-gradient reaches, brown trout abundance was negatively correlated with water depth and the amount of pool habitat ≥ 30.5 cm deep. A different set of variables was correlated with brook trout abundance in moderate-gradient reaches; the only habitat feature positively correlated with abundance was water depth. Among moderate-gradient channels, brown trout standing stock declined as the abundance of bank with an angle $< 90^\circ$, pools with cover and glide habitat increased.

The discriminant function analyses of habitat differences between low-gradient and moderate-gradient reaches identified nine variables that can be used to separate the two channel types: mean shore depth, the percentages of bank with a bank angle $< 45^\circ$, undercut bank, pools formed by woody debris, cobble substrate, trench pools, secondary channel pools and plunge pools. These nine variables were used in a stepwise multiple-regression analysis of all 48 stream reaches to determine which ones may be of most value in accounting for variation in trout standing stocks. Two regression models that accounted for substantial variation in standing stock of trout (S) were identified. The first equation ($R^2 = 0.64$) included undercut bank (U), trench pools (T) and pools ≥ 30 cm deep (P):

$$S = 38.3 + 2.75 U + 3.81 T - 1.40 P$$

The second equation ($R^2 = 0.67$) included trench pools and pools ≥ 30 cm deep, as well as secondary channel pools (S) and mean shore depth (D):

$$S = -11.6 + 2.96 T - 2.47 P - 24.67 S + 21.20 D.$$

These two equations illustrate that habitat variables included in habitat assessment models are to a great degree separating stream reaches into low-gradient and moderate-gradient classes and accounting for variation due to differences between the two classes. When the nine variables was used in stepwise multiple-regression analyses involving only reaches in individual gradient classes, there were fewer variables that accounted for variation in trout standing stocks and the amount of variation that was accounted for was much less. The equation which best accounted for variation in trout standing stocks among low-gradient channels ($R^2 = 0.36$) had only one variable, undercut bank; the best in moderated-gradient channels ($R^2 = 0.15$) had two variables, pools < 30 cm deep and mean shore depth. Less variation in both standing stock estimates and measured values of the habitat variables within a gradient class contributed to the reduced ability of the habitat variables to account for variation in standing stock.

Discussion

Channel morphology, cover, substrate, and habitat types differed between low-gradient (0.1-1.4%) and moderate-gradient (1.5-4.0%) channels sampled in MBNF. We also found differences in standing stocks of trout in channels with low and moderate gradients. We believe the greater standing stocks of trout in low-gradient reaches was due to a greater abundance of pool habitat and cover in these reaches. Total pool habitat of all types was more abundant in low-gradient reaches (mean = 41% of transect points) than in moderate-gradient reaches (mean = 30%). Also within low-gradient reaches, cover within pool habitat—undercut bank and aquatic vegetation—tended to be more abundant than in moderate-gradient channels.

Measures of the nine habitat variables that we found to discriminate between low-gradient and moderate-gradient channels are frequently found in trout-habitat models developed in the central Rocky Mountains. For example, they are incorporated in the cover and substrate attributes of the habitat quality index of Binns and Eiserman (1979), the overhead bank cover and in-stream rubble-boulder-aquatic vegetation variables of the trout cover rating of Wesche (1980), the overhead bank cover and deep water

components of the modified habitat suitability index model for brown trout by Wesche *et al.* (1987), as well as the substrate and undercut bank variables in the production and biomass models of Scarnecchia and Bergersen (1987). We believe that these variables in the various habitat models are to a great degree accounting for natural changes in habitat resulting from differences in channel gradient.

Our data show that habitat features correlated with trout abundance differ between low-gradient and moderate-gradient channels, as well as between brook trout and brown trout. We believe that the separation of stream segments into reaches with similar gradient may enable the identification of features related to salmonid abundance that are otherwise obscured by variation over a wider range of gradient. Habitat models that predict salmonid abundance should define the range of channel gradient to which they are applicable, and perhaps be developed for specific gradient classes or channel types, as

well as defining the species of trout for which they are applicable.

Accessibility of streams to the public in southeastern Wyoming has been related to trout standing stocks (Wesche *et al.* 1987), with standing stocks declining as accessibility increases. We expect that the trout standing stocks among our study sites were greater than in many other streams in MBNF because the sites tended to be remote without nearby road access, thus fished less. Comparison to data from Binns and Eiserman (1979), Chisholm (1985) and Lanka (1985) confirm this belief.

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Terrestrial Wildlife of the Hanford Site: Past and Future

Abstract

The undeveloped land of the U.S. Department of Energy's Hanford Site provides habitat suitable for a few shrubsteppe animal species whose populations are diminishing elsewhere in eastern Washington, primarily due to the conversion of native stands of vegetation to crop plants. To sustain isolated remnant populations in the future requires information on the habitat requirements of each species. The balance between the extent of natural perturbations, such as wildfire, and the human-induced vegetational changes, such as conversion of stands of native vegetation to crop plants or maintenance of grasses instead of shrubs and grasses to provide more livestock forage, has long-term implications for sustaining threatened and endangered species as well as other native wild animals in semiarid eastern Washington and the shrubsteppe region in general. The Hanford Site, by virtue of its large size (1400 km²) and its conservative use of land, provides a refugium for native wildlife populations in the absence of farming and/or livestock grazing.

Introduction

Wildlife populations inhabiting the 1400 km² of mostly undeveloped land that the Hanford Site now occupies received little or no scientific attention during the years following the advent of regional livestock grazing (circa 1850) and crop cultivation (circa 1880).

In 1943, the land was acquired by the federal government as a site for the production of nuclear materials (Figure 1). The sparse resident human population was relocated, livestock grazing and farming ceased, and the general public was excluded from using the land. The impact of a century of livestock grazing, irrigated and dryland agriculture, and urbanization (two small towns, Hanford and White Bluffs) upon native wildlife populations was not scientifically documented.

Following the relocation of the human population from the Hanford Site, abandoned agricultural fields became self-colonized by a few species of weedy annual plants. These plants, all Eurasian introductions, are now persistent members of the flora. Cheatgrass, *Bromus tectorum*, tumble mustard, *Sisymbrium altissimum*, jagged chickweed, *Holosteum umbellatum*, yellow salsify, *Tragopogon dubius*, and wild lettuce, *Lactuca serriola*, are especially abundant. Re-invasion of the abandoned fields by native plants has been a slow process, mostly because of the intense competition for soil water and nutrients provided by the aliens (Daubenmire 1970, 1975; Rickard and Sauer 1982; Rickard and Rogers 1983).

For the purpose of this review, shrubsteppe habitat consists of stands of desert shrubs with an understory consisting mostly of grasses. Shrubsteppe wildlife species are those that can successfully breed and reproduce using the resources provided mostly by shrubsteppe plant communities.

Mature shrubsteppe plant communities on the Hanford Site are usually dominated by big sagebrush, *Artemisia tridentata*, with scattered stands of antelope bitterbrush, *Purshia tridentata*, rabbitbrush, *Chrysothamnus nauseosus*, spiny hopsage, *Grayia sponosa*, or greasewood, *Sarcobatus vermiculatus*. The most abundant native grasses are bluebunch wheatgrass, *Agropyron spicatum*, Sandberg's bluegrass, *Poa sandbergii*, needle-and-thread, *Stipa comata*, Indian ricegrass, *Oryzopsis hymenoides*, and prairie junegrass *Koeleria cristata*. Native forb species include balsamroot, *Balsamorhiza careyana*, lupine, *Lupinus* spp., long-leaved phlox, *Phlox longifolia*, hawksbeard, *Crepis atriobarba*, scarlet globemallow, *Sphaeralcea munroana*, and evening primrose, *Oenothera pallida*, among others. The few native trees, cottonwoods, *Populus* spp., and willows, *Salix* spp., are restricted to the wet shoreline of the Columbia River and the few spring streams in the Rattlesnake Hills.

Before 1960, cattle had grazed the land adjacent to these spring streams for many years, suppressing the growth of the woody plants. When cattle grazing was terminated by fencing, the streamside vegetation recovered quickly (Rickard and Cushing 1982).

Exotic deciduous trees were planted and irrigated around farm houses for shade and as

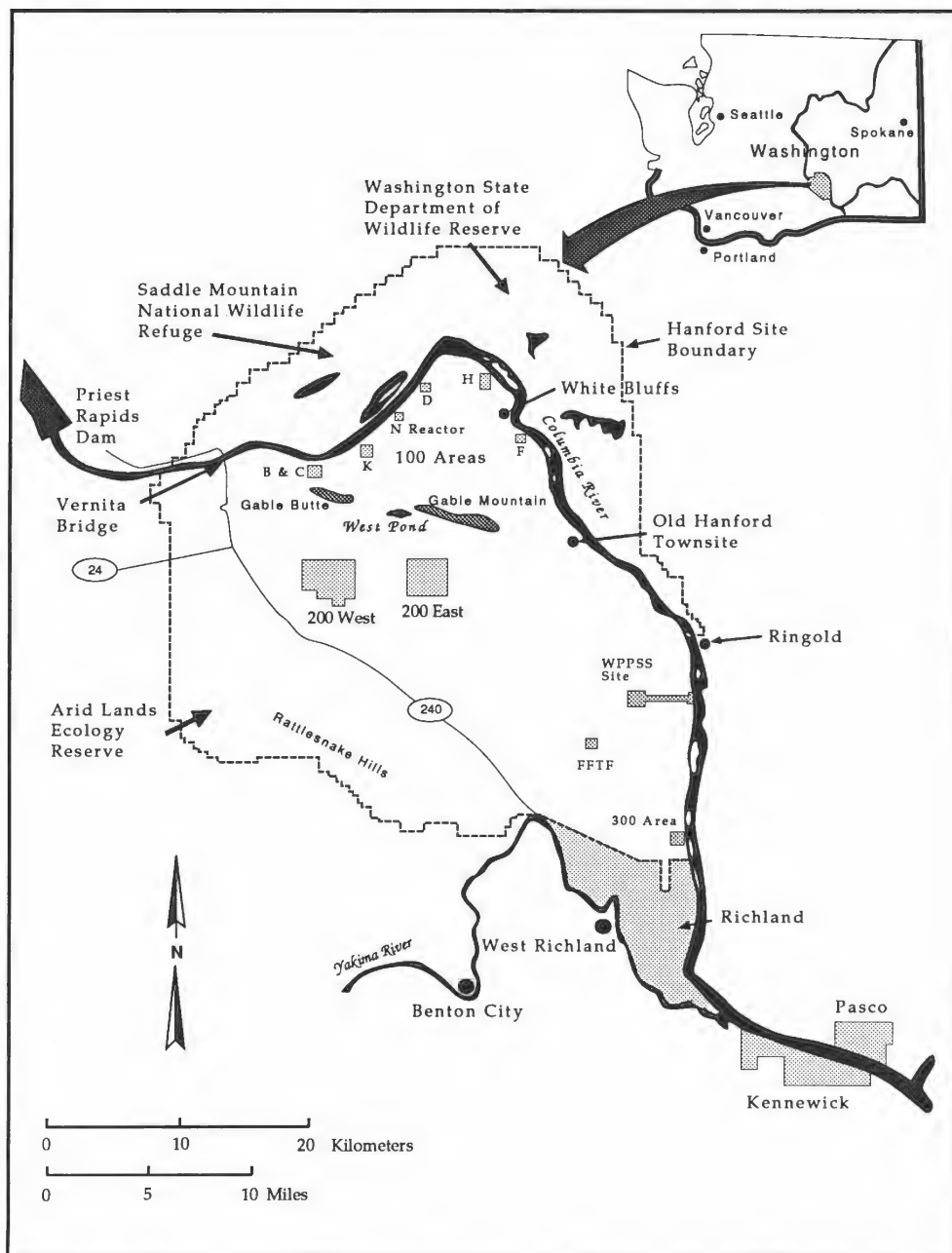


Figure 1. Outline Map of the U.S. Department of Energy's Hanford Site.

windbreaks by residents in the decades before 1943. These trees, mostly black locusts, *Robinia pseudoacacia*, and Siberian elms, *Ulmus pumila*, have not been artificially irrigated since the residents were relocated. Many trees have died, but others are still alive, although they do not reproduce by seedlings.

The large buildings associated with nuclear materials production are clustered at widely spaced locations on the Hanford Site. The reactor buildings (100 Areas) are all situated on the western shoreline of the Columbia River (Figure 1). The chemical separation buildings are located in the 200 East and 200 West Areas near the center of the Hanford Site. The 300 Area, located in the extreme southeastern corner, contains the uranium fuel fabrication facilities as well as numerous other buildings associated with laboratory research. Other building clusters include the Fast Flux Test Facility (FFTF) and the commercial nuclear power stations, WNP-1, 2 and 4, owned by the Washington Public Power Supply System (WPPSS). All building clusters are connected by roadways, railroad tracks, and electrical transmission lines. However, most of the land between the clusters is undeveloped and provides stands suitable for sustaining populations of shrubsteppe birds, mammals, reptiles, and amphibians.

The Arid Land Ecology (ALE) Reserve is a special area of relatively undisturbed land (260 km²) located in the southwestern sector of the Hanford Site (Figure 1 and Figure 2). There are no industrial buildings on the reserve. The ALE reserve was designated as an environmental research area in 1967.

Land Use and Shrubsteppe Wildlife

Land use on the Hanford Site over the last 45 years has not been changed as much as has the surrounding land. In 1952, irrigation water was delivered to the Columbia Irrigation Project, and irrigated crops today occupy thousands of hectares of formerly shrubsteppe habitat (Figure 3). Although the many lakes and seeps formed by irrigation waters have benefited wildlife, such as waterfowl, it has been detrimental to local populations of most native terrestrial species by destroying their habitats.

The shrubsteppe birds, mammals, and reptiles that have been most adversely affected by

agricultural land use have been identified by the Washington Department of Wildlife (1987) and the U.S. Fish and Wildlife Service (1985). Those species thought to be in most need of protection, and that are known or thought to inhabit the Hanford Site, are listed below:

Birds

Sage grouse, *Centrocercus urophasianus*
Sage sparrow, *Amphispiza belli*
Sage thrasher, *Oreoscoptes montanus*
Loggerhead shrike, *Lanius ludovicianus*
Long-billed curlew, *Numenius americanus*
Swainson's hawk, *Buteo swainsoni*
Ferruginous hawk, *Buteo regalis*
Burrowing owl, *Athene cunicularia*

Mammals

Merriam's shrew, *Sorex merriami*
Pygmy rabbit, *Sylvilagus idahoensis* (?)

Reptiles

Striped whipsnake, *Masticophis taeniatus*

The Hanford Site provides habitat suitable for wide-ranging species, including elk, *Cervus elaphus*; mule deer, *Odocoileus hemionus*; coyote, *Canis latrans*; and black-tailed jackrabbits, *Lepus californicus*. These wild animals are usually not tolerated at all, or their populations are artificially suppressed to low-levels, if they inhabit or intrude upon farmlands because of the damage they can do to crops, in the case of the herbivores, and to livestock, in the case of coyotes.

Habitat Conservation and Breeding Shrubsteppe Birds

Habitat conservation is believed to be the key to maintaining breeding populations of shrubsteppe birds. Plants provide nesting sites, perches, and shelter from weather as well as herbage, seeds, insects, and other foods. Sage grouse, *Centrocercus urophasianus*, are rarely seen on the Hanford Site today. In recent years, a few widely separated groups of two to three birds have been seen in the Rattlesnake Hills on the ALE Reserve. Even in the long-time absence of livestock grazing, a purposeful sagebrush eradication program, and recreational hunting, the future of sage grouse on the Hanford Site does not appear promising. Extensive wildfires on the Hanford Site since 1980 have destroyed thousands of hectares of sagebrush stands, and sagebrush itself is believed to be a critical



Figure 2. Rattlesnake Hills on the Arid Lands Ecology (ALE) Reserve; Long-billed Curlew and Badger.

element in sage grouse habitat (McAdoo and Klebenow 1979).

Chukar, *Alectoris chukar*, populations are centered around permanent springs, especially those located in the rough topography of the Rattlesnake Hills on the ALE reserve. At present, the chukar, an alien introduction, is more abundant than the native sage grouse. Chukars forage upon the green shoots and seeds of cheatgrass. The great abundance of cheatgrass on the Hanford Site provides food for chukars during most of the year. However, in the occasional years of deep, persistent snow cover there may be short-term food shortages, as deep snow covers the short-statured cheatgrass plants and especially seeds dropped on the ground.

Long-billed curlews select sparse, mixed stands of Sandberg's bluegrass and cheatgrass for nesting (Allen 1980). Such stands occur in places where fire has destroyed the shrubs or on

some of the abandoned cultivated fields that support sparse stands of cheatgrass.

Historically, nest sites for tree-nesting raptorial birds have been limited on the Hanford Site. Before human settlement, trees were probably scarce and restricted to very narrow zones along the Columbia River and the spring streams on the ALE Reserve. Farmers had planted shade and fruit trees, mostly within a few kilometers of the Columbia River, in the years before 1943. In later years, trees were planted around the few military installations and industrial facilities located in the interior of the Hanford Site. These artificially established trees now provide most of the nest sites for common ravens, *Corvus corax*, black-billed magpies, *Pica pica*, Swainson's hawks, *Buteo swainsoni*, red-tailed hawks, *Buteo jamaciensis*, and American kestrels, *Falco sparverius* (Olendorff 1975, Fitzner 1980a). The number of trees that are suitable for nesting appears to be important in determining Swainson's

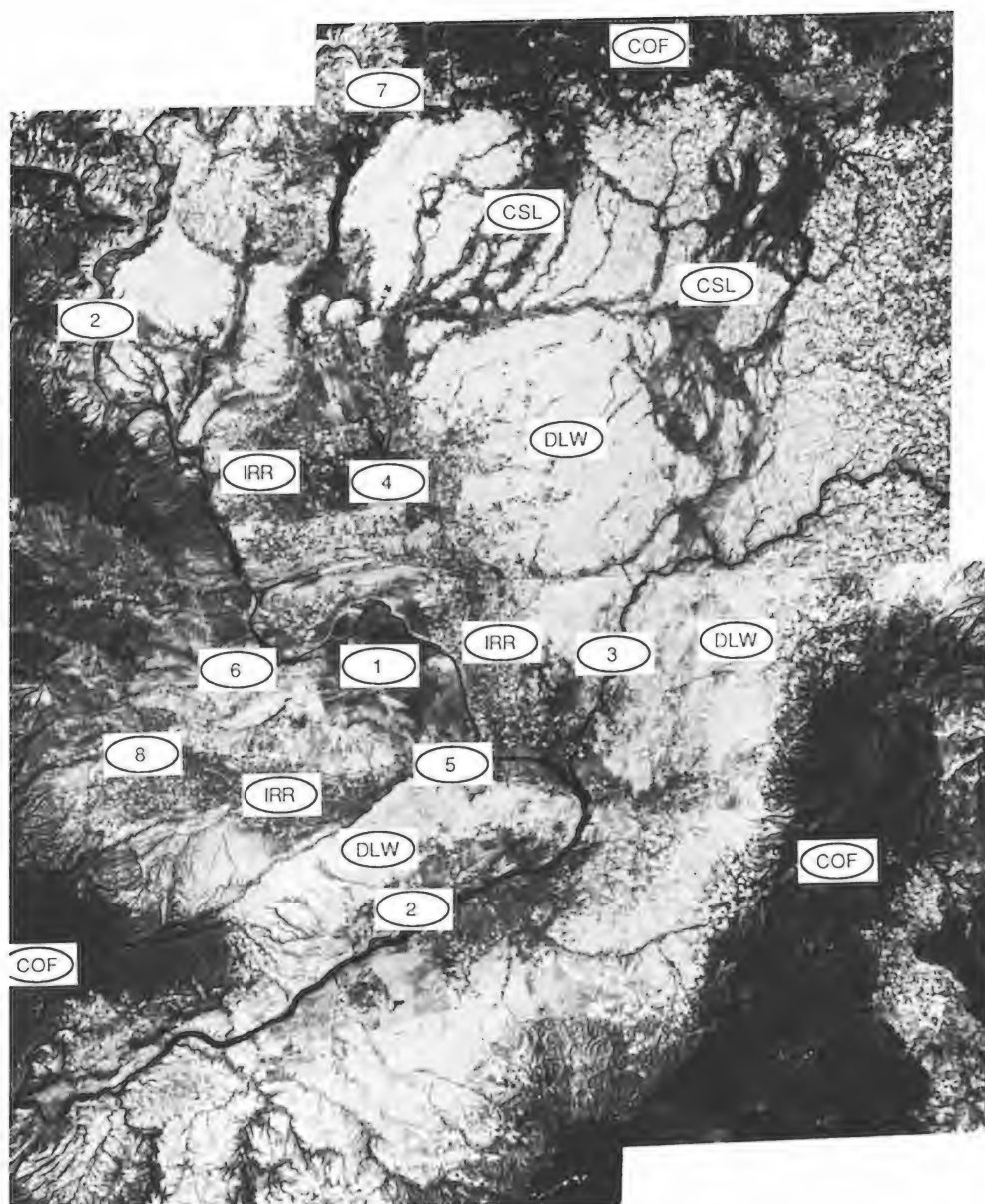


Figure 3. Satellite Image of Southeastern Washington and Adjacent Oregon Showing the Extent of Cultivated Land Surrounding the U.S. Department of Energy's Hanford Site. IRR = Irrigated Land, DLW = Dryland Wheat, COF = Conifer Forest, RRL = Rangeland, and CSL = Channeled Scabland. 1 = Hanford Site Rangeland, 2 = Columbia River, 3 = Snake River, 4 = Potholes Reservoir, 5 = Richland, 6 = Priest Rapids Dam, 7 = Grand Coulee Dam, and 8 = Yakima.

hawk distribution and abundance throughout semi-arid eastern Washington (Tank 1985, Poole *et al.* 1988).

Although cliffs that are suitable for raptor nesting are scarce on the Hanford Site, they do provide nesting locations for prairie falcons, *Falco mexicanus*, red-tailed hawks, and ravens. Electrical transmission towers and utility poles located on the Hanford Site have created artificial nesting platforms for ravens, red-tailed hawks, and ferruginous hawks (Olendorff 1975, Fitzner 1980a). Nesting populations of red-tailed hawks, ferruginous hawks, and common ravens have expanded greatly since 1978, largely through the use of powerline transmission towers as nest sites (Fitzner 1980b).

Western meadowlarks, *Sturnella neglecta*, sage sparrows, and horned larks, *Eremophila alpestris*, are the most abundant of the breeding shrubsteppe passerine birds on the Hanford Site. The most comprehensive study of passerine birds is that of Rotenberry and Wiens (1978), conducted in a sagebrush-bluebunch wheatgrass stand on the ALE Reserve. Total density ranged between 206 and 291 birds per km² over a four-year period.

Although burrowing owls, sage thrashers, and loggerhead shrikes are also present as breeding shrubsteppe birds, studies have not been made to determine their nesting abundance and distribution.

Shrubsteppe Mammals

Elk were not resident on the Hanford Site or elsewhere in the shrubsteppe region of eastern Washington until the early 1970s when a small, self-established herd took up residence on the ALE Reserve (Rickard *et al.* 1977). The herd today numbers about 90 individuals, and the breeding and foraging activities have been mostly confined to the ALE Reserve (McCorquodale *et al.* 1986). The increase of the elk herd from only a few animals in 1972 is attributed to lack of predator mortalities to calves, the absence of shooting, the lack of livestock as competitors for the available forage plants, and the virtual absence of threatening human disturbance during the spring calving period. Although elk, like cattle, depend on only a few spring streams on the ALE Reserve as permanent sources of drinking water, they tend not to congregate and

linger in herds near drinking water sources as cattle do. In summer, elk seek water mostly at night and bed during midday hours, usually at locations more than 2 km from water sources (McCorquodale *et al.* 1986). Elk are also more conservative of water use than cattle, and they tend to forage over much wider areas (Petron 1987).

In recent months elk have strayed from the ALE Reserve and have damaged newly planted fruit trees on adjacent private lands. The damage done to fruit trees by elk has created a need to determine the capacity of the ALE Reserve to provide enough forage to sustain an elk herd of 100 or so animals without permanently damaging the vegetative cover and also to remove excess animals.

No quantitative estimates have been made of the size of the mule deer population on the Hanford Site, but the population is several times greater than the elk population. Deer that are born on the Hanford Site travel off site and are sometimes killed by hunters on adjacent properties (Hedlund 1975). The deer population has not increased to the point where they have damaged crops as has been the case with elk. Coyote predation on new-born fawns is thought to be an important factor in suppressing the mule deer population on the Hanford Site (Steigers and Flinders 1980).

The coyote is the largest mammalian predator inhabiting the Hanford Site. Information on the seasonal movements of radio-collared coyotes has been obtained by Springer (1982) and Crabtree (doctoral dissertation in preparation). Mated coyotes have relatively small activity ranges, but transients are highly mobile, often travelling beyond the boundaries of the Hanford Site.

No population data exists concerning bobcats, *Lynx rufus*, but they are thought to be much less abundant than coyotes. Badgers, *Taxidea taxus*, are also present, but in small numbers. Badgers are of special concern to maintaining the integrity of low-level radioactive waste burial trenches because of their inherent capacity for deep burrowing with possible exhumation of buried waste materials.

Black-tailed jackrabbits on the Hanford Site are generally more abundant at elevations less than 290 m above mean sea level. They also tend to avoid areas that are devoid of sagebrush from

burning or past agricultural practices. Cyclic fluctuations in jackrabbits during the 45-year existence of the Hanford Site are not apparent. This contrasts with the shrubsteppe lands of Idaho National Engineering Laboratory in southeastern Idaho, which periodically experiences marked cyclic fluctuations (Stoddart 1983). The factors responsible for the absence of marked cyclic population fluctuations on the Hanford Site are unknown. There is some evidence suggesting that cheatgrass is not palatable to jackrabbits; thus, an abundant forage plant may not be available to them (Uresk 1978).

White-tailed jackrabbits, *Lepus townsendi*, are rarely seen on the Hanford Site, and the few sightings that have been made are all near the summit of the Rattlesnake Hills (1000 m above sea level) on the ALE Reserve (Fitzner pers. comm.).

The Great Basin pocket mouse, *Perognathus parvus*, is by far the most numerous mammal on the Hanford Site, occurring in all dryland habitats ranging from near the Columbia River to the crest of the Rattlesnake Hills (Hedlund *et al.* 1975, O'Farrell *et al.* 1975, Rogers and Hedlund 1980, Gano and Rickard 1982, Marr *et al.* 1988). At higher elevations in the Rattlesnake Hills the pocket mouse is generally less abundant in trap catches than the deer mouse, *Peromyscus maniculatus*. At low elevations pocket mice usually comprise more than 80 percent of the small mammal trap catches. Northern grasshopper mice, *Onychomys leucogaster*, are widespread, but their numbers are very low in comparison to deer mice and pocket mice. In addition to mice, Townsend's ground squirrels, *Spermophilus townsendi*, can be locally abundant in certain stands of shrubsteppe vegetation (Hedlund and Rickard 1981). Small mammals provide the food base for badgers, coyotes, and nesting hawks.

Three relatively rare, sagebrush-dependent species of small mammals are known or thought to inhabit shrubsteppe habitats on the Hanford Site. These are Merriam's shrew, the sagebrush vole, *Lagurus curtatus*, and the pygmy rabbit. Little is known about the distribution of shrews, but sagebrush voles were most often trapped at elevations above 400 m (O'Farrell 1975). Pygmy rabbits were present in a sagebrush stand on the ALE Reserve in the years before 1979 (Fitzner pers. comm.). Since then, several large wildfires have destroyed many square kilometers of sage-

brush and the rabbits have not been seen since. Patches of sagebrush habitat, superficially similar to the site that burned, did not burn, but these patches have not yet been thoroughly searched for the presence of pygmy rabbits.

Ord's kangaroo rats, *Dipodomys ordii*, and Washington ground squirrels, *Spermophilus washingtonii*, may occur on the Hanford Site, but there are no validated sightings.

Reptiles and Amphibians

The abundance and distribution of reptiles and amphibians on the Hanford Site have received little scientific investigation. Side-blotched lizards, *Uta stansburiana*, occur in sagebrush-dominated as well as shrub-free burned areas and are by far the most abundant of the Hanford Site lizards (Marr *et al.* 1988). Northern sagebrush lizards, *Sceloporous graciosus*, have been collected from sand dune habitats, dominated by bitterbrush (Marr *et al.* 1988). Short-horned lizards, *Phrynosoma douglassi*, occur all across the Hanford Site (Marr *et al.* 1988, Fitzner pers. comm.), but in small numbers.

Great Basin gopher snakes, *Pituophis melanoleucus*, western yellow-bellied racers, *Coluber constrictor*, and northern Pacific rattlesnakes, *Crotalus viridis*, are the most abundant snakes on the Hanford Site (Marr *et al.* 1988). Striped whipsnakes rarely have been sighted (Fitzner pers. comm.). The presence of the desert night snake, *Hypsiglena torquata*, has not been confirmed.

The abundance and distribution of amphibians on the Hanford Site has not yet been determined. However, Great Basin spadefoot toads, *Spea intermontana*, occur near Rattlesnake Springs on the ALE Reserve (Marr *et al.* 1988).

Wildfire

Wildfire destroys shrubs, especially sagebrush, bitterbrush, and spiny hopsage. Many years may be required for the self-restoration of shrub stands. However, greasewood shrubs are not easily killed by burning, and the stands essentially can be self-restored within a few years (Rickard and McShane 1984). A lightning-caused fire destroyed almost all the sagebrush in a sagebrush-bluebunch wheatgrass stand on the ALE Reserve, resulting in a reduction in the number of sage sparrows in succeeding years. Densities of horned

larks on the burned area initially increased, then declined (Rotenberry and Wiens 1978).

Little is known about the size of sagebrush stands that are acceptable as nesting habitats for sage sparrows. Sullivan (1987) investigated passerine species' richness in sagebrush patches of various sizes in the Columbia Basin north of the Hanford Site, finding higher densities of sage sparrows in large contiguous sagebrush stands than in stands of less than 615 ha. However, passerine species' richness was more highly correlated with the number of shrub species present than with stand size.

Some evidence exists that natural burning of sagebrush-bunchgrass stands has little immediate impact on pocket mouse and ground squirrel populations (Hedlund and Rickard 1981). Most Hanford Site wildfires occur in July and August when the vegetation is at seasonal dryness. Ground squirrels remain below ground in burrows in summer, and they do not re-emerge until late winter. When they do become surface active, in later winter or early spring, there is an abundance of fresh green grass, especially Sandberg's bluegrass. The perennial grasses associated with sagebrush stands are usually capable of restoring shoot productivity in the first growing season after burning (Uresk *et al.* 1976). Pocket mice are active above ground in the summer fire season (O'Farrell *et al.* 1975), but they can escape direct burn and heat mortality by remaining in their burrows. Summer wildfires probably do not destroy all the seeds that are stored in the litter and surface soil, and at least some seeds are probably available to pocket mice even in the first few days and weeks after summer burning. Following summer burning, a new seed crop of Sandberg's bluegrass is ripe by mid-April, and cheatgrass seeds are ripe by mid-May, thereby providing an abundant food source for pocket mice throughout summer and autumn months.

Non-burrowing animals are probably more vulnerable to direct fire mortality than are the burrowing animals. Adult deer, elk, coyotes, and bobcats are usually mobile enough to avoid most wildfires, but jackrabbits may be killed. The long-term damage of burning to jackrabbit populations is perceived as the loss of mature sagebrush shrubs, which provide forage, concealment from predators (golden eagles, bobcats, and coyotes), and shade from the hot summer sun. Deer populations can also be indirectly affected by wildfires

over the long term because burning kills bitterbrush shrubs that provide browse. The self-recovery of bitterbrush stands following summer burning appears to be a slow process, especially if the burned areas are extensive (Rickard and Rogers 1983).

Human-Imposed Habitat Changes

Shrubsteppe habitats in eastern Washington are under continuous assault from a multitude of human activities that result in the continuing diminishment or even extirpation of local populations of some native avian and mammalian shrubsteppe species. Some large-scale, human-induced landscape alterations (e.g., shrub removal by mechanical means and herbicide applications) are designed to economically eliminate shrubs and improve the site for livestock-palatable grasses. The resulting grass-dominated habitats are not acceptable to some nesting birds (Wiens and Rotenberry 1985, Wiens *et al.* 1986).

In shrubsteppe areas of southern Idaho, crested wheatgrass, an alien perennial bunchgrass, has been artificially established on vast acreages of land to produce forage for livestock. These stands provide only marginal habitat for native shrubsteppe wildlife (Reynolds 1978). Springtime livestock grazing can also be harmful to ground nesting birds through trampling of nests (Reynolds and Trost 1981).

The exotic trees artificially planted on the Hanford Site do not re-establish themselves through seedlings. Unless some effort is made to artificially replace these trees, the number of acceptable nesting places for tree-nesting birds such as Swainson's hawks will slowly diminish as the trees age and eventually die. Artificial nest structures could provide acceptable nesting sites for some tree-nesting birds. One advantage of artificial structures is that they can be located at strategic locations appropriately spaced to accommodate home ranges and territory requirements, if these are known from previous research.

Shrubsteppe Wildlife in Relation to Radionuclide Contamination on the Hanford Site

From 1943 to the early-1960s, little attention was paid to terrestrial wildlife on the Hanford Site except as biological indicators of airborne releases of radionuclides from the operating

industrial buildings. The radionuclide of most concern to non-occupational human health was iodine-131 released into the air during the operation of the chemical separation buildings in the 200 Areas. Some of the radioactive iodine was deposited on the leaves of plants, which in turn were eaten by black-tailed jackrabbits. Jackrabbits were routinely collected from various locations on the Hanford Site to determine the pattern of dispersion of iodine-131 because it was assimilated in the thyroid glands and could be detected and measured by the instruments available at that time (Hanson 1960, 1962).

Today, the terrestrial environmental monitoring conducted for the Hanford Site includes collecting chuckars, California quail, *Callipepla californica*, ring-necked pheasants, *Phasianus colchicus*, and Nuttall's cottontails, *Sylvilagus nuttalli*, to obtain flesh and bone samples for cesium-137 and strontium-90 analyses (Price *et al.* 1985). Tissues of road-killed mule deer are also included in the environmental sampling protocol.

As an adjunct to the routine monitoring programs, Eberhardt and Cadwell (1984) recorded the daily and seasonal movements of radio-collared mule deer. Deer that habitually drank from and foraged around ponds that had received controlled releases of radionuclides in aqueous streams had slightly higher concentrations of radiocesium in their flesh than did deer that drank from and foraged along the Columbia River.

The regurgitated castings of hawks and owls that roost on the Hanford Site had measurable concentrations of radionuclides of Hanford Site origin, indicating that the prey items (mostly rodents) eaten by the hawks and owls had access to arrays of radionuclides indicative of the different chemical processes used in the nuclear fuel industry (Cadwell and Fitzner 1984).

The most unusual case of terrestrial wildlife and radionuclide dispersal involved a burrowing mammal in conjunction with black-tailed jackrabbits (O'Farrell and Gilbert 1975). A burrowing mammal dug into a shallow land burial trench and brought radioactive material to the soil surface. The exhumed materials were then ingested by jackrabbits, and radionuclides became dispersed in the rabbits' feces and urine during the normal movements of free-roaming individuals.

Today, engineering designs for low-level

radioactive waste burial trenches incorporate "biological barriers" constructed to deter burrowing mammals and deep-rooting plants from contacting buried wastes. Layers of loose rock (to deter animal burrowing) and the downward moisture percolation are capped with fine-textured soil to encourage shallow root penetration. Rainwater stored in the surface soil is returned to the atmosphere via evaporation and plant transpiration processes during the growing season, thereby restricting the amount of downward percolation of moisture through the soil cap and possible transport beyond the Hanford Site boundaries by groundwater.

Future

The long-term land use of the Hanford Site has a somewhat uncertain future. However, it does not appear likely that the undeveloped land surrounding the industrial buildings will be used for livestock grazing or agricultural crops, at least until the existing inventory of high-level radioactive waste stored in underground tanks during the years of nuclear materials production is permanently isolated from the biological environment. This will probably require many years of effort. Environmental monitoring will be continued and can be expected to include sampling of wildlife populations and documentation of the status of ever-changing wildlife populations, especially rare, threatened or endangered species, and those species of great aesthetic or recreational importance.

The lands surrounding the Hanford Site are expected to continue to be intensively cultivated, with irrigated acreages continuing to expand at the expense of the remnant stands of native vegetation. Stands of native vegetation will become increasingly restricted to thin, rocky soils and steep hillsides that cannot be plowed. However, even these places will probably be grazed by livestock. The Hanford Site will serve as a future refuge for remnant populations of native wildlife species in eastern Washington as the surrounding land becomes more intensively used for crop plants, for livestock grazing, and for urban developments.

Wildfires will continue to be an important factor in determining the pattern of distribution of mature shrubs on the Hanford Site. Burning has implications for the long-term conservation

and management of shrub-dependent species of animals such as sage sparrows, sage thrashers, and sage grouse (McAdoo and Klebenow 1979, Castrale 1982) as well as for mule deer and jackrabbit populations. Burning of sagebrush stands appears to provide habitat for nesting long-billed curlews (Figure 2), western meadowlarks, and horned larks, birds that usually select sparse stands of herbaceous plants as nesting

habitat. However, burning is deleterious to nesting sage sparrows, loggerhead shrikes, and sage thrashers, birds that characteristically place their nests in the branches of sagebrush shrubs.

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Northwest Science

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Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

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Announcements

In This Issue

In this issue and with this issue is information about the Northwest Scientific Association and in particular about the upcoming annual meeting. If things go well, this issue will come to you in an envelope together with a variety of information that I hope you will take the time to read through.

To keep costs down and membership current, the annual dues renewal notice is included in this issue. By filling it out and returning your dues now your membership will be extended from its current expiration date. And the Association can reduce the time and expense we have had to spend in the past on membership renewals. Please help by taking a moment now to return your annual dues.

—Editor

Annual Meeting of the Northwest Scientific Association

COME TO CORVALLIS IN THE SPRING! The 1990 annual meeting of the Northwest Scientific Association will be held March 21-23, at LaSells-Stewart Center on the Oregon State University campus.

A highlight of this year's meeting will be a day-long symposium entitled "Environmental Disasters and the Nature of Recovery." It will focus on several recent "natural" disasters, including the Yellowstone fire, the Alaska earthquake, the St. Helen's eruption, and the Alaska oil spill. Each event will be described in colorful presentations, followed by discussions of the ecological processes and time involved as the ecosystems adjust to new conditions.

Other features include:

- The George Fahnestock Memorial Fire Science Symposium
- Mixing Science and Fun—A Wine and Cheese Social
- A day-long field trip to the Oregon Coast (whale watching, sand dunes, shore birds, seafood lunch in Newport)
- A half-day field trip to Finley Wildlife Refuge (heart of Dusky-footed Canadian Goose winter range)
- A wide variety of half day mini-symposia
- Award of student research grants
- Recognition of an outstanding Northwest scientist and the usual chance to hear your colleague's research results two years before they are published!

Spring comes early to the Willamette Valley! Rhododendrons, azaleas, and a variety of flowers will already be blooming. The weather is variable, so you're likely to see a bit of our lovely soft rain, and some sunshine too. The Willamette Valley is between the volcano-studded Cascades and the timber-shrouded Coast Range, so you can plan your spring break to include a favorite winter or spring activity. Skiing is still fine at Mt. Bachelor, Mt. Hood, Hoodoo, or Willamette Pass. The grey whales are migrating along the coast, and waterfowl are abundant along the river and at wildlife refuges. A recent addition to Willamette Valley fun is an enthusiastic maturing wine industry, including vineyards and wine tasting rooms.

We extend a special invitation to students. They are encouraged to give papers, with a reward of a free ticket to the NSA Banquet. At the wine and cheese social, we will make a special effort to introduce students and researchers from various universities and organizations. Remember, abstracts of all papers presented at the meeting are formally published as a supplemental issue of *Northwest Science*.

Mark your calendar now, wrap up that unreported data, and get your abstract in *early* for a change. We're planning a truly fine Northwest Science Meeting for next March! Don't miss it!

Announcements continued on last page

Sheep Production in Coastal Oregon Douglas-fir Plantations¹

Abstract

The recent interest in using biological tools in resource management, together with a desire to use energy sources more efficiently, has increased interest in employing sheep grazing as a silvicultural tool to suppress competing vegetation in commercial conifer plantations. Widespread use of sheep as a biological control agent in forests is currently limited by insufficient numbers of sheep available to forest managers. Few data exist concerning livestock performance in Coastal Oregon Douglas-fir plantations. Without such information, livestock producers are reluctant to commit their current flocks to a silvicultural program or to purchase additional sheep in order to take advantage of this new forage source. The purpose of our study was to document sheep weight gains, death losses, and forage quality (crude protein and digestibility) during the spring-summer grazing season. Data were collected during 1981, 1982, 1984, and 1985 from flocks of 250-900 sheep which grazed coastal Douglas-fir plantations near Alsea, Oregon. Average daily gains of lambs ranged from 95 to 175 g/head/day, while yearling ewes gained 78 g/head/day. Ewes lost an average of 4.5 kg/head in liveweight during the grazing season. Sheep had highest daily gains in spring when forage plants were most nutritious. Livestock death loss, 3 to 5 percent of the flock, was no higher than that reported for flocks grazing in pastures. Our data suggest that increased death loss of herded sheep in coastal forests is not much of a problem. A bigger issue is weight gains, which tended to be lower than those achievable on nearby improved pastures.

Introduction

In the past ten years, there has been renewed interest in reintroducing sheep into cut-over forests in the Pacific Northwest. This interest has been prompted by two factors: the desire to use energy sources more efficiently and the current emphasis on biological tools for resource management in a period of environmental concerns (Hedrick 1975, Doescher *et al.* 1987). Controlled livestock grazing has been shown to (1) reduce the biomass of herbaceous and shrubby vegetation which competes for nutrients and light with timber regeneration (Kosco and Bartolome 1983, Krueger 1983, Sharrow and Leininger 1983), (2) decrease the fire hazard in young plantations (Ingram 1931), and (3) improve big game habitat (Reiner and Urness 1982, Rhodes 1984).

Presently, forest grazing in the Cascade and Coast mountain ranges is limited by the lack of adequate numbers of sheep to efficiently utilize the forage resources now available. Before new permittees will make the large investment required to purchase sheep, questions concerning the forage resources available, expected animal liveweight gains and death losses must be answered. The objective of this study was to provide information on seasonal forage quality and sheep production which livestock operators can

use in assessing the profitability of grazing cut-over forests in the Pacific Northwest.

Materials and Methods

This study was conducted in the Coast Range, approximately 15 km west of Alsea, Oregon, U.S.A. Climate is maritime, with cool, rainy winters and warm, dry summers. Evening and early morning fog is common, even in summer. Most of the approximately 250 cm of precipitation falls as low-intensity rain from October through May (Corliss 1973). Elevation of the study area ranged from 75 to 450 m and the slope varied from 0 to more than 100%.

The major understory vegetation type in the study area is the vine maple-sword fern (*Acer circinatum*-*Polystichum munitum*) community (Corliss and Dyrness 1965). Dominant herbaceous plants include common velvetgrass (*Holcus lanatus*), bentgrass (*Agrostis* spp.), tansy ragwort (*Senecio jacobaea*), and big deer vetch (*Lotus crassifolius*). Current year's growth of phytomass available to sheep ranged from approximately 850 kg/ha in the spring to 3,000 kg/ha in late summer (Leininger and Sharrow 1987).

Seven hundred Columbia ewes and their lambs and 900 Columbia yearling ewes grazed the forest from May to September in 1981 and 1982, respectively. A flock of approximately 250 Suffolk ewes and their lambs grazed from May to September 1984 and again from May to August in 1985. All

¹This manuscript is Oregon Agricultural Experiment Station Technical Paper No. 7334.

sheep were managed as a single flock under the constant supervision of a herder with dogs. A series of small plantations ranging in size from 10 to 40 ha each was grazed. Sheep were moved from plantation to plantation on a predetermined route, spending from 1 to 7 days in each. Stocking rates were approximately 125, 143, 167, and 148 ewe days per hectare in 1981, 1982, 1984, and 1985, respectively.

Sheep liveweight gain was evaluated by weighing a random sample of animals immediately prior to turnout in the forest in May, midway through the grazing season during June and/or July, and at the end of the grazing season in August-September (Table 1). The minimum sample size at each weighing was the number of sheep which yielded a standard error of the mean equal to or less than one kg. Average daily gain (ADG) was calculated as weight change between two dates. Standard errors of ADG were computed using a pooled error derived from dates involved (Steel and Torrie 1980). Death loss and probable cause of death were recorded by the permittee and U.S. Forest Service personnel.

Samples of current year's growth of the major forage plants (Table 3) were collected from within a 30m x 30m ungrazed enclosure in 5 grazed timber plantations which were part of the grazing loop each year. Collections were made in late March-early April 1982 and 1983, and in May, July-early August and October 1981 and 1982. Forage samples were dried at 50°C, then analyzed in duplicate for crude protein using a micro Kjeldahl method (AOAC 1980) and for *in vitro* dry matter disappearance using the two-stage artificial rumen technique of Tilly and Terry (1963). In ad-

dition, percent tannin content of major browse plants was determined using the vanillin-hydrochloric acid method (Burns 1963).

Results and Discussion

Mature ewes with lambs lost an average of 3.4, 1.6, and 5.2 kg/head liveweight during the 1981, 1984, and 1985 grazing seasons, respectively (Table 1). Dry conditions in 1985 caused forage plants to mature early and probably accounted for the large weight loss (5.2 kg/head) that year. During the first half of the grazing season (May through June), ewe weight loss ranged from 10 to 130 g/ewe/day (Table 2). This weight loss was understandable in light of the high nutritional demands placed upon them by lactation. Ewe performance was considerably better during the second half of the grazing season in 1984 and 1985 after lambs were weaned and removed from the forest. In contrast, lambs were not weaned during the 1981 grazing season and ewe weight losses continued to increase across the grazing season as forage plants matured. Yearling ewes without lambs gained 8.6 kg/head during May to July 1982. Their weight changed little during July-September (1.2 kg/head).

Lambs gained 14.2, 10.2, and 4.0 kg/head while on the forest during 1981, 1984, and 1985, respectively. Similar to yearling ewes, liveweight gain of lambs was highest during the first half of the grazing season in 1981. Lambs were removed from the forest in 1984 and 1985 when their rate of gain began to decline.

Sheep weight gains followed seasonal trends typical of animals grazing nonirrigated, western Oregon pastures. Several authors (Sharrow *et al.*

TABLE 1. Liveweight of sheep (kg/head) grazing coastal Oregon Douglas-fir timber plantations.

Class of Livestock	Year	Initial Weight	Final Weight	Grazing Days*	Sample Size
Ewes	1981	58.2 (0.7)	54.8 (0.8)	124	125
Lambs	1981	7.4 (0.2)	21.6 (0.6)	124	125
Yearling Ewes	1982	43.1 (0.5)	52.9 (0.4)	126	100
Ewes	1984	67.0 (0.9)	65.4 (0.8)	135	90
Lambs	1984	30.5 (0.5)	40.7 (0.7)	59	90
Ewes	1985	70.6 (0.9)	65.4 (0.8)	110	75
Lambs	1985	33.3 (0.5)	37.3 (0.7)	42	60

*Grazing days is number of days between initial and final weight measurements and is approximately the length of the grazing season.

Liveweights are mean (standard error).

TABLE 2. Average Daily Liveweight Gains (ADG) of sheep grazing in coastal Oregon Douglas-fir timber plantations.

Class of Livestock	Period	Year	ADG* (g/head/day)
Ewes, Lactating	8 May-3 July	1981	- 10 (20)
Ewes, Lactating	3 July-9 September	1981	- 40 (20)
Lambs, Nursing	8 May-3 July	1981	+ 140 (10)
Lambs, Nursing	3 July-9 September	1981	+ 90 (10)
Ewes, Yearling	11 May-2 July	1982	+ 170 (10)
Ewes, Yearling	2 July-14 September	1982	+ 20 (10)
Ewes, Lactating	8 May-11 June	1984	+ 10 (40)
Ewes, Lactating	11 June-6 July	1984	- 130 (50)
Ewes, Dry	6 July-19 September	1984	+ 10 (20)
Lambs, Nursing	8 May-11 June	1984	+ 180 (30)
Lambs, Nursing	11 June-6 July	1984	+ 160 (40)
Ewes, Lactating	1 May-11 June	1985	- 130 (30)
Ewes, Dry	11 June-18 August	1985	- 50 (20)
Lambs, Nursing	1 May-11 June	1985	+ 100 (20)

*Data are mean (standard error).

1981, Warner and Sharrow 1984) have reported negative weight gains for ewes grazing improved hill pastures in the foothills of the Coast Range during the summer-fall dry feed period (July to November). In contrast, weight gains exceeding 220 g/ewe/day have been reported for sheep grazing cut-over forests (Hall *et al.* 1959, Black and Vladimiroff 1963) and foothill pastures (Sharrow *et al.* 1981, Warner and Sharrow 1984) during the spring green feed period (April through June). Four-year average sheep liveweight gains during spring in our study, - 70 g/ewe/day and + 145 g/lamb/day, are generally lower than the - 10 to - 25 g/ewe/day and + 140 to + 185 g/lamb/day reported for annual grass-clover pasture (Sharrow *et al.*, 1981) or the + 140 to + 180 g/ewe/day and + 200 to + 210 g/lamb/day reported for perennial grass-clover pastures (Sharrow 1983, Warner and Sharrow 1984) in the nearby foothills of the Coast Range. Average ewe weight loss during the summer (- 25 g/ewe/day), however, was generally similar to that from perennial grass-clover pasture in our area, - 10 to - 90 g/ewe/day (Sharrow 1983, Warner and Sharrow 1984).

Seasonal liveweight changes of herbivores, presumably, reflect changes in the quantity and quality of forage available to them. In our study, sheep entered the forest about midway through

the green forage period. Consequently, this reduced the length of grazing time when forage quality was highest and potential livestock liveweight gains the greatest. Rhodes (1984), working in the same area, concluded that an adequate amount of forage phytomass was available to sheep throughout the grazing season. Crude protein (CP) content of forage plants (Table 3) during March to May generally met or exceeded National Research Council (NRC 1975) recommendations for lactating ewes and growing lambs (11% CP). However, only shrubs and some forbs met maintenance protein requirements for dry ewes (9% CP) during the summer and fall (July through September). Digestibility of graminoids and forbs generally decreased across the grazing season as did crude protein. Shrubs had consistently low digestibility regardless of season. Shrub digestibility was never adequate to support lactating ewes, and in most cases was not even sufficient to maintain dry ewes. A variety of phenolic compounds have been found in several common western Oregon shrubs (Li 1974). Tannins in particular are known to affect digestibility of forages by inhibiting rumen microbes (Lohan *et al.* 1981) and by chemically binding with dietary proteins (Reed *et al.* 1982). Tannin levels in the six major browse plants which we examined were sufficiently high to reduce

TABLE 3. Mean percent ($\pm$ S.E.) *in vitro* dry matter digestibility (IVDMD) and crude protein (CP) of selected forage species of Oregon's Coast Range.

Species		Season							
		March		May		July-August		October	
		1982	1983	1981	1982	1981	1982	1981	1982
Graminoids:									
<i>Agrostis</i> spp. ¹	IVDMD	75 ± 1.5	66 ± 2.8	—	64 ± 4.1	—	52 ± 3.0	28 ± 2.0	37 ± 2.1
	CP	17.9 ± 0.5	16.6 ± .03	—	11.6 ± 1.1	—	5.6 ± .07	4.3 ± 0.3	4.3 ± 0.3
<i>Carex hendersonii</i>	IVDMD	31 ± 3.8	42 ± 2.3	47 ± 2.7	49 ± 1.4	41 ± 1.3	42 ± 4.1	38 ± 3.1	25 ± 3.5
	CP	8.1 ± 1.1	8.8 ± 0.4	9.2 ± 0.7	12.2 ± 0.3	8.1 ± 20.5	7.8 ± 0.1	6.7 ± 0.3	6.9 ± 0.1
<i>Dactylis glomerata</i>	IVDMD	70 ± 6.6	73 ± 1.7	69 ± 0.8	75 ± 0.9	53 ± 1.4	58 ± 3.1	32 ± 4.5	36 ± 5.1
	CP	23.0 ± 0.6	21.5 ± 1.0	7.5 ± 0.2	9.6 ± 0.3	5.1 ± 0.1	6.2 ± 0.1	3.9 ± 0.2	6.3 ± 0.5
<i>Holcus lanatus</i>	IVDMD	70 ± 1.2	73 ± 1.7	—	71 ± 2.7	—	46 ± 4.2	30 ± 2.8	41 ± 3.3
	CP	16.0 ± 0.5	16.0 ± 0.4	—	9.7 ± 0.1	—	4.5 ± 0.2	5.2 ± 0.6	8.0 ± 0.4
Forbs:									
<i>Anaphalis margaritacea</i>	IVDMD	76 ± 3.4	62 ± 2.5	52 ± 1.6	60 ± 3.1	43 ± 1.1	46 ± 2.2	30 ± 2.4	31 ± 3.0
	CP	21.6 ± 0.5	24.3 ± 0.6	13.2 ± 1.4	16.3 ± 0.6	8.2 ± 0.5	8.6 ± 0.6	5.5 ± 0.3	5.6 ± 0.4
<i>Lotus crassifolius</i>	IVDMD	48 ± 2.7	61 ± 2.5	47 ± 1.4	53 ± 1.6	28 ± 0.8	23 ± 1.7	38 ± 3.8	16 ± 2.4
	CP	—	41.8 ± 0.5	22.9 ± 0.4	34.2 ± 0.2	15.6 ± 1.1	15.9 ± 0.4	8.9 ± 0.3	10.4 ± 0.8
<i>Scrophularia californica</i>	IVDMD	70 ± 1.8	68 ± 1.3	59 ± 1.6	63 ± 0.6	—	37 ± 2.9	40 ± 5.1	36 ± 6.5
	CP	—	22.3 ± 1.1	13.5 ± .01	12.3 ± 0.1	—	9.4 ± 0.1	9.8 ± 1.3	11.9 ± 1.8
<i>Senecio jacobaea</i>	IVDMD	75 ± 2.2	77 ± 1.7	37 ± 5.0	80 ± 1.0	67 ± 2.8	68 ± 4.6	48 ± 4.4	65 ± 6.7
	CP	16.5 ± 0.6	18.0 ± 0.4	11.8 ± 0.1	13.1 ± 0.9	5.2 ± 0.1	8.1 ± 1.4	7.0 ± 0.7	9.0 ± 0.8
<i>Acer circinatum</i>	IVDMD	—	—	51 ± 3.0	54 ± 5.6	45 ± 2.1	42 ± 1.7	41 ± 3.2	34 ± 2.4
	CP	—	—	12.2 ± 0.1	19.4 ± 0.8	9.7 ± 0.9	11.8 ± 0.6	4.3 ± 0.4	5.9 ± 0.3
<i>Alnus rubra</i>	IVDMD	48 ± 2.8	42 ± 1.2	41 ± 0.7	43 ± 1.0	35 ± 1.7	25 ± 1.0	40 ± 3.4	23 ± 3.6
	CP	—	25.9 ± 0.9	14.6 ± 0.1	23.1 ± 0.1	17.3 ± 0.2	15.8 ± 0.2	14.4 ± 0.3	—
<i>R. parviflorus</i>	IVDMD	47 ± 2.7	45 ± 2.9	43 ± 1.4	44 ± 2.6	35 ± 1.9	32 ± 1.1	41 ± 2.7	32 ± 0.9
	CP	25.1 ± 0.8	22.1 ± 0.6	11.3 ± 0.4	18.7 ± 2.0	7.8 ± 0.3	9.7 ± 0.3	7.7 ± 0.3	8.1 ± 0.4
<i>R. spectabilis</i>	IVDMD	36 ± .28	37 ± 1.9	36 ± 1.6	33 ± 0.9	29 ± 1.7	24 ± 1.1	37 ± 3.1	22 ± 1.5
	CP	24.5 ± 0.6	20.5 ± 0.8	14.5 ± 0.4	20.7 ± 0.5	7.9 ± 0.2	9.7 ± 0.3	8.3 ± 0.3	6.8 ± 0.2
<i>R. ursinus</i>	IVDMD	39 ± 2.0	45 ± 1.7	44 ± 0.8	48 ± 3.5	33 ± 1.7	29 ± 1.7	37 ± 2.1	25 ± 0.9
	CP	21.4 ± 0.8	20.5 ± 1.0	12.4 ± 0.3	19.2 ± 1.0	8.0 ± 0.2	8.8 ± 0.2	6.6 ± 0.2	7.7 ± 0.3

¹Includes *Agrostis exarata* and *A. tenuis*.

digestibility of forage by ruminants (Reed *et al.* 1982). Observed tannin levels ranged from 1.3 to 4.6 percent of forage dry matter, being thimbleberry (*Rubus parviflorus*), 1.3 percent, salmonberry (*Rubus spectabilis*), 1.5 percent, California dewberry (*Rubus ursinus*), 2.0 percent, vinemapple 2.6 percent, and red alder (*Alnus rubra*) 4.6 percent. Sheep tended to increase their consumption of shrubs during the summer as grasses and forbs matured (Leininger and Sharrow 1987). Increased intake of shrubs during the summer and fall probably contributed to poor livestock performance during that period.

Death losses were generally low, being 28 ewes (3%) plus 25 lambs (5%) in 1981, 21 ewes (5%) in 1982 and 20 ewes and lambs (4%) in 1984. These losses are similar to the 3% annual loss during the grazing season reported for sheep and goats on all Forest Service lands (U.S. Fish and Wildlife Service 1978), but generally lower than the 8.4 to 19.5 percent and 6.5 to 12.5 percent annual death loss reported for ewes and lambs, respectively, in Oregon (Gee *et al.* 1977, de Calesta 1979).

As with other forests in the Pacific Northwest where sheep have grazed transitory range

(Ingram 1928, Harshman 1979, Phelps 1979), losses in this study from predation were low. Three sheep were taken by coyotes in 1982 and 5 in 1984. No verified losses of sheep to predators occurred in 1981. Higher death losses from predators have been reported during the grazing season for other types of rangeland in Oregon (de Calesta 1979, Terrill 1988) and for Forest Service lands in general (U.S. Fish and Wildlife Service 1978).

Harshman (1979) speculated that (1) grazing dry ewes which were less susceptible to coyote predation and (2) grazing in areas where predators had not had access to sheep for 40 years were major reasons for the lack of predation on sheep which grazed cut-over forest land in the Cascade Range. In our study, we believe these reasons, plus the presence of a herder with dogs and the relatively short time spent in each plantation, largely explain the low number of animals lost to predators.

Management Implications

Sheep grazing should be initiated as early in the spring as vegetation and soils permit. The breeding season should be scheduled to produce early (December-February) lambs. This will maximize the time that lambs graze during the green feed period when forage quality is highest. The potential for sheep browsing on conifer regeneration must also be considered when setting the grazing season (Sharrow and Leininger 1983).

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Traditional forest grazing schemes which have been employed in much of the U.S. Intermountain Region allow livestock to follow green feed up the mountain as the grazing season progresses. Since the Coast Range, like many other low-elevation forests, lacks the elevational change required for this type of livestock management, we suggest plantations be grazed in a rotational sequence which maximizes the time that animals spend grazing forage regrowth in previously grazed plantations during the latter half of the summer. Our data also suggest that lambs be removed from the forest by mid-summer. Since our brush plants are generally too low in digestibility to support livestock weight gains, use of sheep to control brush will generally involve some loss of potential livestock performance. Forest managers should consider sharing the economic benefits of biological brush control with livestock owners. In some areas, this has been done by paying a fee for use of the livestock.

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The Petrology and Vapor Phase Mineralogy of Rhyolite and Tuffs from Garnet Hill, White Pine County, Nevada

Abstract

Garnet Hill, located in the Robinson mining district, east central Nevada, is a small isolated Cenozoic tuff-rhyolite complex with near-surface vapor phase crystallization. The F-content, major element chemistry, petrology and vapor phase mineralogy of this complex were examined. The rhyolite commonly has vesicles and lithophysae lined with vapor phase drusy quartz and almandine-spessartine garnet. A few vesicles are lined with sanidine, stilbite or calcite. Both the tuff and rhyolite contain phenocrysts of smoky quartz, sanidine, biotite, plagioclase and zircon. Major element chemistry, tectonic setting and size indicate that the Garnet Hill complex is similar to other high-silica Cenozoic rhyolites. The tuff represents the initial explosive stage of eruption, followed by the emplacement of the rhyolite as a lava flow or dome, and the movement of escaping vapor through the cooling body. Most of the vapor moved along fractures parallel to the flow banding, crystallizing quartz, garnet and sanidine at an early high temperature (perhaps approaching 500°C) stage of alteration, followed by a low temperature (50-300°C) stage forming calcite and stilbite. Garnet Hill vapor phase mineralogy is similar to other Cenozoic high-silica, F-rich topaz rhyolites of Western United States. The lower fluorine content and less complex vapor phase mineralogy of Garnet Hill rocks are the major differences that separate them from topaz rhyolites. Garnet Hill's average of 550 ppm F per rock sample is less than one-tenth that of a topaz rhyolite. The significance of these findings is the determination of the origin of the beautiful almandine-spessartine garnets which have been collected by amateur and professional mineralogists for over 100 years. These garnets crystallized directly from a relatively low-fluorine vapor.

Introduction

Garnet Hill is a small, 1.5 x 2.2 km, isolated rhyolite complex located three miles west of Ely, Nevada, in the Robinson Mining District. The Garnet Hill complex is on the northern edge of an extensive area of Cenozoic high-silica ash flow tuffs extending from Reno, Nevada, to Milford, Utah (Stewart *et al.* 1977). The district consists of Devonian to Permian miogeosynclinal sedimentary rocks folded into a northwest-trending overturned anticline cut by six bedding plane thrust faults. The anticline was intruded during the Early Cretaceous (103-123 Ma) by monzonite and quartz monzonite porphyry stocks with which mineral deposits of the Ely area are associated. During early mid-Tertiary time the entire area was fragmented by normal faults (Ridge 1972, James 1976, Westra 1982). Bedded tuffs and coarse rhyolite agglomerates were formed during the Oligocene and were followed by flows and small intrusive rhyolites. Pabst (1938) described the Garnet Hill rhyolite as the youngest igneous complex in the area, with a probable Pliocene age. Brokaw *et al.* (1973) mapped one fault with a displacement of up to 1.5 km cutting the north-

west side of the complex. The age of the complex is most likely 37 Ma, the K-Ar age McDowell and Kulp (1967) reported for an intrusive rhyolite in the Liberty Pit located two miles southwest of Garnet Hill.

The Garnet Hill rhyolite was mapped as "younger rhyolite" on the Geologic Map of the Ruth Quadrangle by Brokaw *et al.* (1973). Hollabaugh and Purcell (1987) separated this unit into the Garnet Hill rhyolite and an underlying crystal-lithic tuff (Figure 1).

Alteration mineral assemblages formed by hydrothermal solutions or vapor phase activity are common in rhyolites. Quartz and sanidine are common vapor phase minerals in many rhyolites. Examples of rhyolite complexes of similar size to Garnet Hill with equally extensive vapor phase crystallization are Ruby Mountain, Colorado (Van Alstine 1969, Schooler 1982), and Shingle Butte, Strawberry Butte, Lava Mountain and Burnt Mountain in the northern Elkhorn Mountains, Montana (Smedes 1966). Many mineral alteration assemblages in rhyolites such as those at the Valles Caldera, New Mexico (Goff *et al.* 1985, Charles *et al.* 1986, Hulen and Nielson

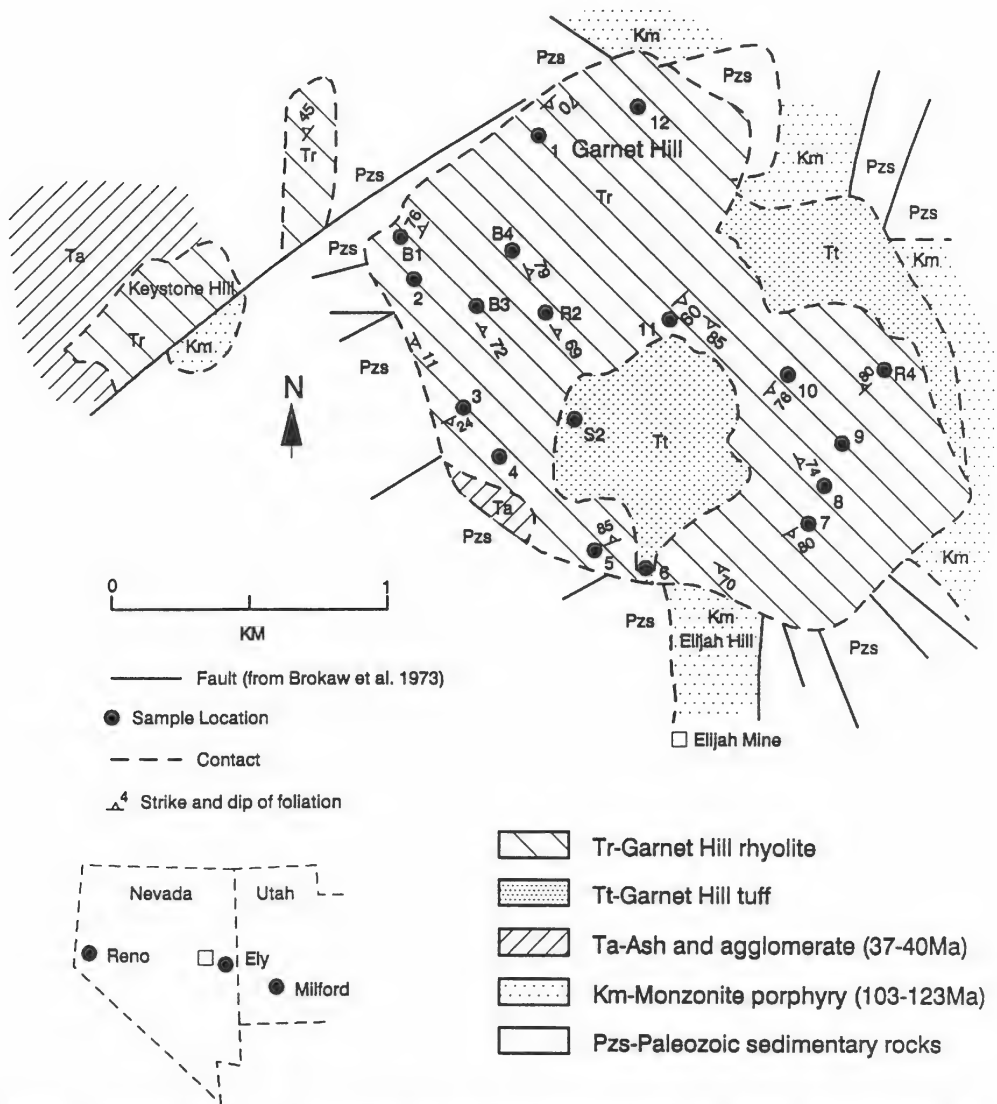


Figure 1. Generalized geologic map of the Garnet Hill complex in eastern Nevada, showing sample locations (modified from Brokaw *et al.* 1973, Hollabaugh and Purcell 1987). Flow banding indicates vent location is near map station 2.

1986) are due to hydrothermal solutions and not vapor phase activity. The hydrothermal minerals formed by geothermal systems in rhyolites include mixed-layer illite-smectite, illite/sericite, smectite, kaolinite, chlorite, epidote, albite and calcite at the Baca geothermal system, Redondo Dome, Valles Caldera, New Mexico (Hulen and Nielson 1986) and adularia, albite, alunite, alunogen, anatase, gypsum, halotrichite, illite,

kaolinite, montmorillonite, pyrite, quartz, rozenite, sulfur and szomnokite at Sulphur Springs, Valles Caldera (Charles *et al.* 1986).

Vapor phase alteration commonly occurs in topaz-rhyolites (Staatz and Carr 1964; Lindsey 1977, 1982; Burt *et al.* 1982; Christiansen *et al.* 1986), but these rhyolites are F-rich with > 1 percent F while the Garnet Hill rhyolite is F-poor. The topaz-rhyolites contain topaz visible in hand

specimens but no topaz occurs at Garnet Hill. The vapor phase mineralogy (e.g. topaz, bixbyite, pseudobrookite, red beryl, hematite, garnet, opal, quartz, fluorite, calcite, and feldspar) and mineral deposits (e.g. Be, F, and U) of 26 topaz rhyolites within the western United States are described by Christiansen *et al.* (1986). Huspeni *et al.* (1984) and Ruiz *et al.* (1985) describe the fluorite deposits within the F-rich high silica rhyolites of the Sierra Madre Occidental, Mexico. Garnets in rhyolites also occur at Canterbury, New Zealand (Wood 1974), in the Cerberian Cauldron, Central Victoria, Australia (Birch and Gleadow 1974), and on the Trinity Peninsula, Antarctica (Hamer and Moyes 1982). Green and Ringwood (1968) describe the origin of garnet phenocrysts in calc-alkaline rocks. Keith *et al.* (1986) use almandine-spessartine garnet of unique chemistry to correlate intrusive porphyry and ash-flow tuff in the Wah Wah Mountains of Utah.

In this paper the mineralogy, petrology, major element chemistry and vapor phase alteration of the Garnet Hill complex are described.

Analytical Methods

Eighteen samples were collected for petrographic and chemical analysis. Major element abundances were determined by atomic absorption analysis using U.S.G.S. rocks as standards. Loss on ignition (LOI) was determined by heating at 900°C for four hours (Christiansen *et al.* 1984). Fluorine was measured by the method of Kanisawa (1979) with a Fisher Accumet Selective ion analyzer using a Corning fluoride electrode, reference electrode and standard F solutions from Corning Glass Works. Each fluorine analysis was repeated three times and the average values are reported in Table 1. Oxide percentages plotted in Figure 2 were normalized to 100

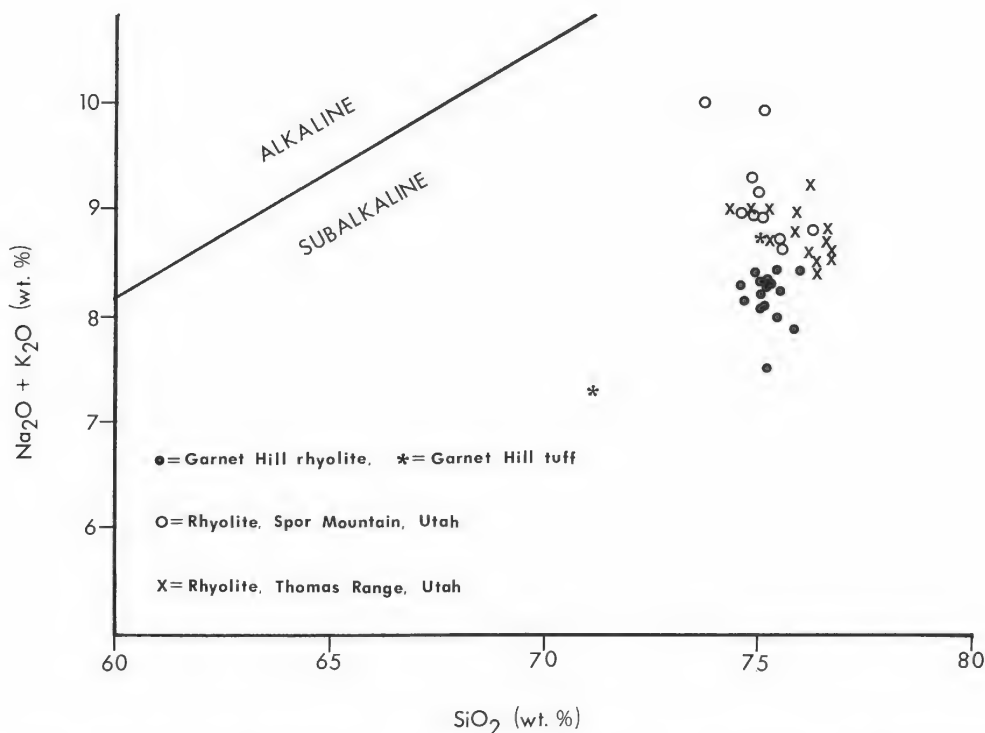


Figure 2. Variation of weight percent $\text{Na}_2\text{O} + \text{K}_2\text{O}$ versus SiO_2 for the Garnet Hill tuff and rhyolite. Topaz rhyolites from Spor Mountain and Thomas Range, Utah (Christiansen *et al.* 1984) are shown for comparison.

TABLE 1. Whole-Rock Chemical Analyses of Garnet Hills Rhyolites.*

Sample Number	(Oxide Weight %)										H ₂ O ^{&}	F [@]
	SiO ₂	TiO ₂	Al ₂ O ₃	FeO [#]	MnO	MgO	CaO	Na ₂ O	K ₂ O	Total		
1	73.5	0.17	13.6	1.26	0.06	0.16	1.02	3.38	4.65	97.8	2.45	540
2	74.4	0.17	12.9	2.24	0.08	0.06	1.20	3.47	4.65	99.2	0.46	730
3	72.8	0.16	12.6	1.99	0.08	0.19	1.69	3.35	4.56	97.4	0.28	730
4	73.0	0.16	13.1	1.52	0.08	0.19	1.08	3.29	4.74	97.2	5.36	250
5	73.9	0.16	13.1	1.57	0.07	0.12	1.08	3.47	4.65	98.1	0.66	245
6-tuff	70.8	0.35	14.3	2.55	0.05	1.09	3.00	3.43	3.83	99.4	2.05	910
7	75.1	0.15	14.0	1.48	0.08	0.46	1.14	2.99	4.56	99.9	1.30	700
8	74.0	0.15	13.3	1.44	0.06	0.29	1.07	3.35	4.65	98.3	0.30	670
9	73.2	0.14	13.0	1.49	0.07	0.34	1.07	3.40	4.56	97.3	1.32	435
10	73.8	0.14	13.1	1.45	0.08	0.40	1.14	3.35	4.47	97.9	1.85	655
11	74.7	0.13	13.2	1.66	0.06	0.27	1.20	3.52	4.84	99.6	0.40	495
12	76.1	0.13	13.6	1.45	0.07	0.10	1.14	3.26	4.66	100.5	0.22	415
B1	73.1	0.35	11.5	3.70	0.16	0.11	0.94	3.56	4.63	98.1	0.20	190
B3	73.8	0.34	12.0	1.67	0.08	0.14	0.94	3.47	4.72	97.2	0.33	805
B4	72.8	0.33	12.0	1.87	0.08	0.14	1.82	3.54	4.63	97.2	1.23	610
R2	74.2	0.31	11.5	1.70	0.06	0.33	2.03	3.61	4.72	98.5	1.74	330
R4	73.5	0.31	12.4	1.68	0.13	0.19	1.06	3.71	4.29	97.3	0.92	475
S2-tuff	73.7	0.34	12.1	2.18	0.12	0.14	0.89	3.86	4.72	98.1	0.31	745

CIPW Norms in Weight Percent (from analyses recalculated to 100%)**

	q	or	ab	an	c	di	hy	wo	mt	il
1	33.69	28.07	29.28	5.16	1.23	—	1.88	—	0.36	0.32
2	32.78	27.72	29.62	6.00	0.01	—	2.90	—	0.64	0.32
3	32.22	27.66	29.11	6.07	—	2.22	1.84	—	0.58	0.30
4	33.27	28.84	28.69	5.51	0.57	—	2.37	—	0.45	0.30
5	33.18	28.01	29.95	5.46	0.42	—	2.22	—	0.45	0.30
6-tuff	27.63	22.81	29.19	12.33	—	2.20	4.46	—	0.72	0.66
7	36.36	26.95	25.30	5.66	2.05	—	2.94	—	0.42	0.28
8	33.77	27.95	28.85	5.41	0.84	—	2.48	—	0.42	0.28
9	33.22	27.72	29.62	5.46	0.57	—	2.73	—	0.43	0.27
10	34.08	27.01	28.94	5.75	0.69	—	2.83	—	0.42	0.27
11	32.01	28.72	29.95	5.83	—	0.15	2.61	—	0.48	0.25
12	35.68	27.42	27.50	5.66	1.07	—	2.03	—	0.41	0.25
B1	31.78	27.89	30.72	1.83	—	2.59	3.43	—	1.07	0.68
B3	33.85	28.72	30.21	3.35	—	1.27	1.44	—	0.49	0.66
B4	31.63	28.19	30.80	3.27	—	4.60	—	0.30	0.55	0.65
R2	32.05	28.37	31.05	0.87	—	5.21	—	1.36	0.49	0.61
R4	33.14	26.06	32.24	4.77	—	0.55	2.13	—	0.49	0.61
S2-tuff	31.07	28.49	33.34	1.89	—	2.30	1.63	—	0.64	0.66

*Atomic Absorption Analysis done at West Georgia College.

#Total Fe as FeO.

&Water determined by LOI.

@F in ppm, determined by ion selective probe.

**Total Fe recalculated as 20% Fe₂O₃ and 80% FeO.

Note: q = quartz, or = orthoclase, ab = albite, an = anorthite, c = corundum, di = diopside, hy = hypersthene, wo = wollastonite, mt = magnetite, il = ilmenite

percent after removal of water. Rock names follow the International Union of Geological Sciences (IUGS) classification method (Streckeisen 1979). Energy dispersive x-ray analysis (EDAX) on a scanning electron microscope (SEM) was used to determine feldspar compositions and to check for zoning in garnets. Powder X-ray diffraction with a Philips APD 3520 was employed to determine mineralogy of fine grained matrix material.

Petrology and Major Element Chemistry

The Garnet Hill complex consists of two distinct, mappable units. The lower unit, a crystal-lithic tuff which is friable, unstratified and slope-forming, covers the south-central one-quarter of the complex. The pink to gray crystal-rich tuff contains 25 to 32 volume percent phenocrysts in a glassy matrix. The modal mineralogy is: quartz 17 percent, feldspar 5 percent, biotite 4.2 percent, opaques 0.5 percent and glass 73.3 percent. Quartz phenocrysts (0.1 to 5 mm) are euhedral (bipyramidal) to anhedral and may have a round outline. Euhedral feldspar phenocrysts (0.1 to 4 mm) are zoned plagioclase and sanidine. Up to 20 percent of the feldspars are broken. Biotite is euhedral with well formed hexagonal outlines and light to dark brown pleochroism. Euhedral zircons and Fe-Ti oxides occur as inclusions within phenocrysts. The tuff has no garnets or vapor phase alteration.

The overlying rhyolite is gray to pink with prominent flow banding and vesicles. It forms the tops of seven hills within the complex and weathers to thin platy slabs or to honeycomb structures. It is phenocryst-poor and has a spherulitic cryptocrystalline groundmass. X-ray diffraction studies indicate the groundmass is composed primarily of quartz and sanidine feldspar. Phenocrysts of quartz, sanidine, plagioclase, biotite, garnet and opaques make up 0 to 5 percent of the rhyolite. Large sanidine crystals are anhedral and highly fractured. The euhedral to anhedral garnet phenocrysts are intergrown with quartz.

The vesicles are commonly aligned with the flow banding and locally contain lava stalactites (Smedes 1966). Widespread vapor phase alteration has resulted in crystallization of drusy quartz in many vesicles and rare euhedral garnet and sanidine in a few vesicles. One vesicle contained

euhedral calcite and stilbite crystals. Structures in the flow banding vary in scale from one cm to several meters or more. Garnets were collected from several areas having subparallel flow banding that extends for 3 m.

Whole-rock chemical analyses of 18 Garnet Hill rhyolite and tuff samples are given in Table 1. These data are plotted on a total $\text{Na}_2\text{O} + \text{K}_2\text{O}$ versus SiO_2 diagram (Figure 2) with data from Topaz Mountain and Spor Mountain, Utah (Christiansen *et al.* 1984). The Garnet Hill rhyolites plot in the rhyolite field on the IUGS QAPF diagram (Streckeisen 1979). Major element chemistry of Garnet Hill rocks is very similar to other high silica rhyolites, including topaz rhyolites. Within the Garnet Hill data set there is little chemical diversity. The tuffs have lower average silica contents (72.25 wt. %) than the rhyolite (73.87 wt. %). The average fluorine content of the tuff (829 ppm) is slightly higher than that of the rhyolite (517 ppm). The higher biotite content of the tuff accounts for this difference. These fluorine contents are well below the 1,600 to 12,500 ppm found in topaz rhyolites from Topaz Mountain and Spor Mountain (Christiansen *et al.* 1984). The presence of corundum (C) in half of the whole rock norms (Table 1) indicates that the Garnet Hill rhyolites are slightly peraluminous.

Vapor Phase Alteration

The Garnet Hill rhyolite has been subjected to vapor phase alteration resulting in the growth of quartz, garnet (Figure 3) and euhedral sanidine crystals up to 5 mm long and 1 mm across (Figure 4) in vesicles. The greatest concentration of vapor phase minerals occurs along fractures parallel to the flow banding within the rhyolite. The garnet compositions are 67.6 percent almandine, 27.3 percent spessartine, 4.3 percent grossular and 0.8 percent pyrope (Hollabaugh and Purcell 1987). Very few garnets are phenocrysts; 99 percent of them are found as euhedral crystals in vesicles. Most of those found in the vesicles display only half the trapezohedral faces, and petrographic examination of the garnets at their point of attachment shows that the garnet "crystals" extend into the rhyolite as mixtures of garnet and quartz.

A second stage of alteration resulted in the crystallization of calcite and stilbite (Figure 5) in the rhyolite. The amount of stilbite formed was very minor. Calcite is associated with the stilbite.

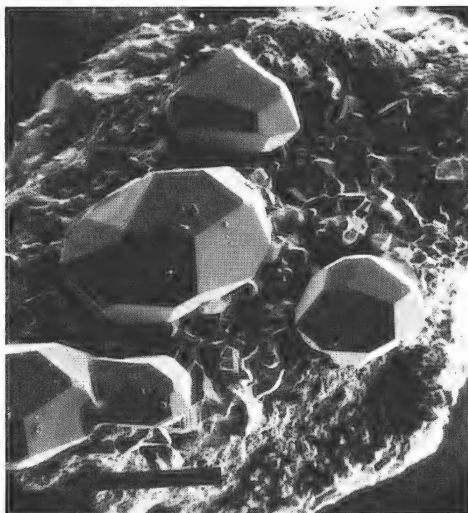


Figure 3. SEM photomicrograph of amandine-spessartine garnet from Garnet Hill. Length of scale bar is 1 mm.



Figure 4. SEM photomicrograph of sanidine crystals in vesicle from Garnet Hill rhyolite. Note the twinned crystal (left-center). Scale bar is 0.1 mm.

Discussion

Formation of Garnet Hill rhyolite and tuff

Figure 6 shows the principal stages in the development of the Garnet Hill complex; A. Formation of ash-flow tuff, B. Emplacement of Garnet Hill rhyolite as a small flow or dome, and C. Vapor phase mineralization and low tempera-



Figure 5. SEM photomicrograph of stilbite crystals in vesicle from Garnet Hill rhyolite. Length of scale bar is 0.1 mm.

ture zeolite-calcite alteration. Before the first stage a small magma body intruded into the area. Crystallization of zircon, magnetite, plagioclase, biotite, sanidine, and quartz formed a crystal-rich layer that was the source area for the tuff. The crystallization of mineral phases can cause an increase in the water content at the top of the magma chamber and volatile over-saturation which subsequently triggers eruption (Blake 1984).

The similarity of the whole rock chemistry and mineralogy of tuff and rhyolite suggest the same source. The eruptive episode commenced with emplacement of tuff. The rhyolite was emplaced as a flow or dome. The initial ash eruption tapped the upper crystal-rich part of the magma. Similar episodes of activity have occurred in topaz rhyolites at Spor Mountain and Thomas Range, Utah (Christiansen *et al.* 1984), the small rhyolite complexes south of Helena, Montana, described by Smedes (1966) and Ruby Mountain near Nathrop, Colorado (Van Alstine 1969, Schooler 1982).

Origin of Vapor Phase Minerals

The origin of vapor phase mineralogy in topaz rhyolites has been described by Burt *et al.* (1982). During cooling and devitrification vapor is released which ascends upward through the cooling

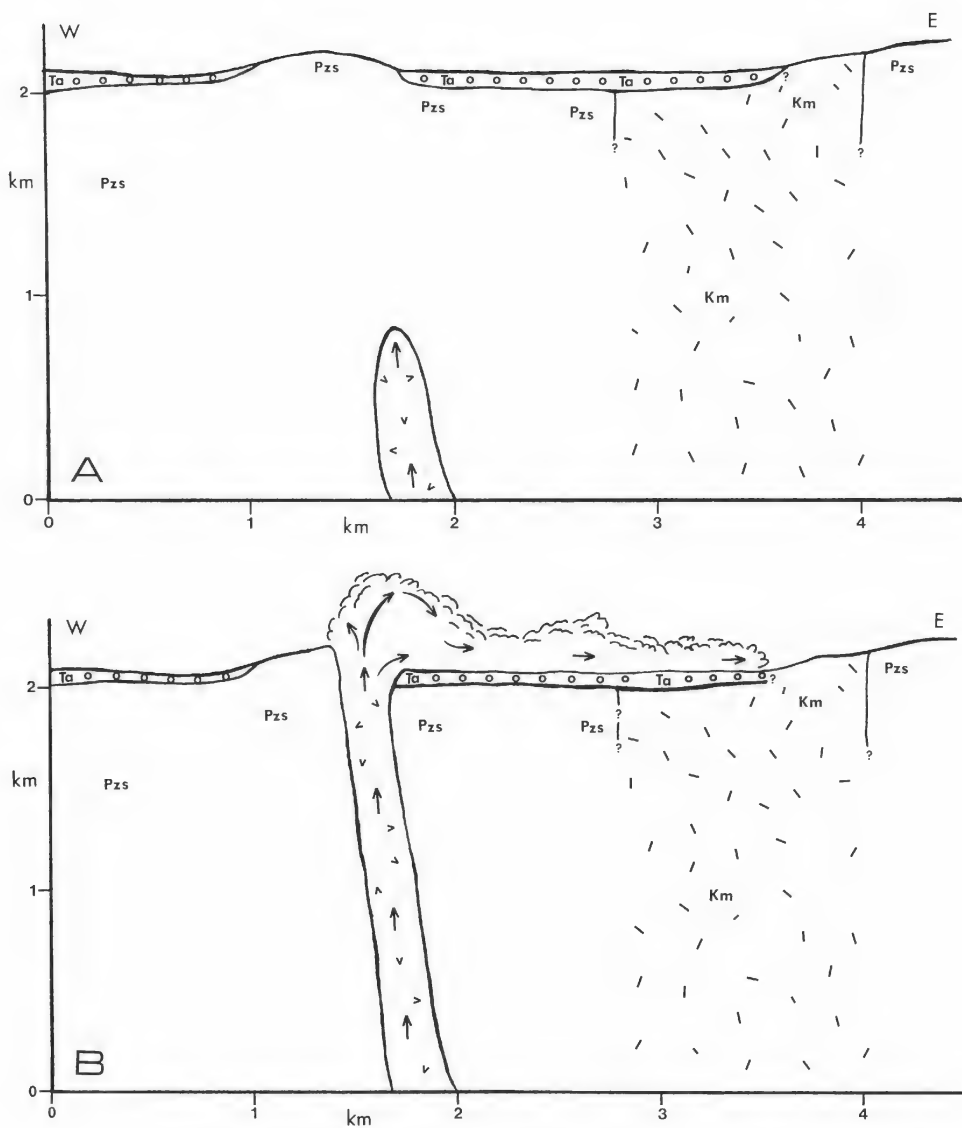
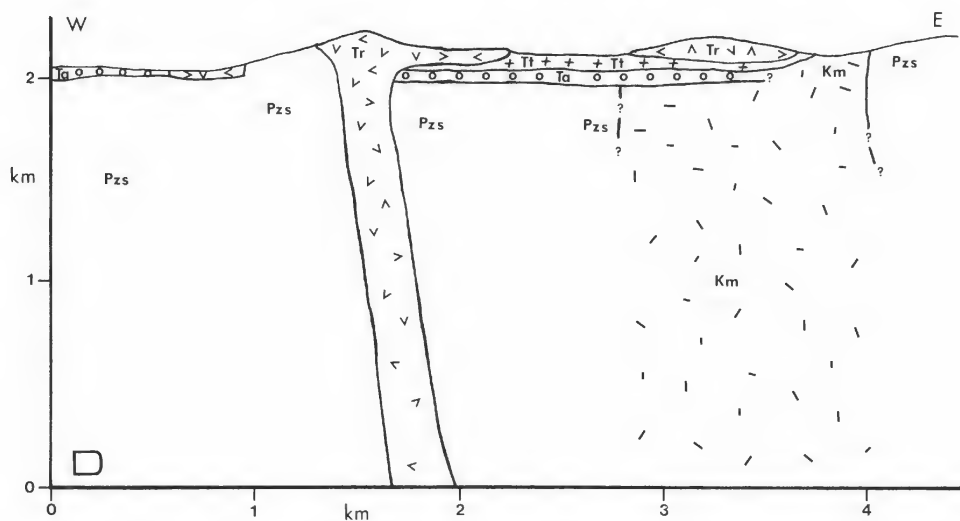
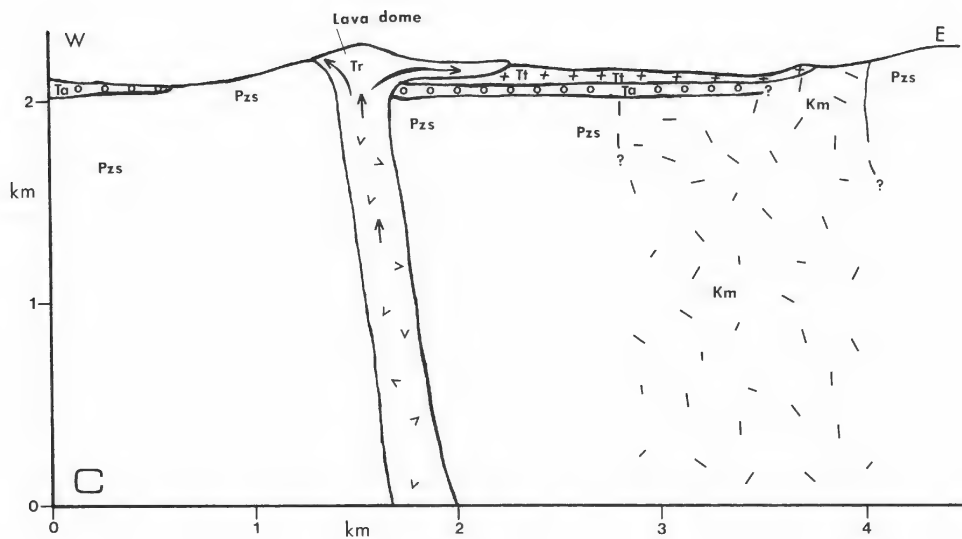


Figure 6. Schematic diagram illustrating eruptive history of the Garnet Hill complex: A. Intrusion of crystal rich rhyolite pipe, B. Initial eruptive blast and pyroclastic flow and deposition of Garnet Hill tuff (Ta).
(Figure 6 continued, next page)



- ▼ Tr—Garnet Hill rhyolite
- + Tt—Garnet Hill tuff
- Ta—Ash and agglomerate (37-40 Ma)
- ▭ Km—Monzonite porphyry (103-123 Ma)
- Pzs—Paleozoic sedimentary rocks

Figure 6. (Continued) C. Eruption of Garnet Hill lava dome or plug (Tr); shortly thereafter, hot vapors escape from cooling lava and/or underlying magma pipe and deposit vapor phase quartz, garnet and sanidine, and D. Post eruption faulting has offset the northwest side of the complex. Low temperature alteration forms stilbite and calcite.

unit. K, Na, Al, Si, Fe and Mn are partitioned into the vapor phase. A minimum temperature of 500°C for the formation of vapor phase minerals at Black Rock, New Mexico, and Thomas Range, Utah, is indicated by the high Fe content of the bixbyite and the presence of pseudobrookite instead of rutile (Lufkin 1976). The euhedral vapor phase sanidine in the vesicles at Garnet Hill also suggests high temperatures (Yund and Tullis 1983). The garnets at Garnet Hill were probably formed at about 500°C. The mixture of garnet and quartz within the rhyolite changes into pure garnet as the crystal emerges into the vesicle. The garnet-quartz mixture must have been forming as the vesicle formed and as the vesicle developed the garnet grew into the open space. Garnet may have first formed in the viscous lava as it solidified. Solidification temperature is unknown. However, the low F content (e.g. lack of topaz and 190 to 910 ppm F versus the 1600 to 12500 ppm F of the Thomas Range and Spor Mountain, Christiansen *et al.* (1984)) indicates a higher solidification temperature at Garnet Hill than the 850 to 600°C temperature reported for topaz rhyolites (Burt *et al.* 1982).

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Complexing of cations with F in topaz rhyolite magmas is considered to play an important role in metal ion transport (Lindsey 1982). The lower F content of Garnet Hill rhyolite places a limit on the amount of vapor phase ion transport. The less complex vapor phase mineralogy at Garnet Hill reflects the slower rate of ion transport.

The stilbite and calcite assemblage was formed after the vapor phase mineral assemblage. Zeolites commonly form in igneous rocks undergoing hydrothermal alteration over the temperature range 300°C (Hay and Sheppard 1977) to 40°C (Hay 1977).

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Mass Movement of River Ice Causes Severe Tree Wounds Along the Grande Ronde River in Northeastern Oregon

Abstract

In eastern Oregon and Washington, ice forms in streams and rivers during prolonged periods of freezing temperatures. When rapid thawing occurs, large pieces of ice detach, move down waterways, strike trees, and cause damage. Tree wounds caused by ice movement were categorized on black cottonwood (*Populus trichocarpa* Torr. and Gray), willows (*Salix* spp.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). Tree wounds ranged from 63 to 14,066 cm² which resulted in 3 to 100 percent bark removal at about 1.4 m above the ground. Wounded conifers did not have appreciable decay. Ice movement caused either direct mortality of important shrub species, such as mountain alder (*Alnus incana* (L.) Moench), or indirect mortality through wounding and subsequent infection by canker fungi. This indicates that such damage may seriously alter these riparian zones and thus affect the many associated resources.

Introduction

Riparian zones are disproportionately important to many resources including minerals, water, roads, grazing, wildlife and fish, and recreation (Thomas *et al.* 1979). In eastern Oregon and Washington, ice forms in streams and rivers during periods of prolonged freezing temperatures. After rapid thawing, large pieces of ice move down waterways and may form an ice jam when blocked by obstructions in the river. As water rises behind these jams, flooding occurs allowing large blocks of river ice, often several meters across, to float from normal river channels onto flood plains. This ice collides with trees and shrubs along the riverbank, often with enough force to remove tree bark, break shrubs or small trees, and snap larger trees.

Decay in living trees and shrubs is associated primarily with stem wounds (Etheridge and Craig 1976, Aho 1977, Shigo 1986). Wounds can either activate dormant spores of decay fungi or serve as entry courts for fungal spores. Wounds on trees in developed recreation areas are of particular concern, because decay associated with such wounds can increase the probability of tree failure and result in destruction of property or loss of human life. Riparian zones are often choice areas for developed recreation sites.

The primary objective of this study was to determine incidence and severity of tree wounding caused by ice movement at three sites along the Grande Ronde River in northeastern Oregon.

Methods

In October 1986, three sites along the Grande Ronde River in northeastern Oregon were examined for tree wounding caused by mass movement of river ice. The sites were near Hilgard State Park, Red Bridge State Park, and an area between these two parks. At these three sites, all wounded trees were examined for tree and wound characteristics. The following data were collected from each wounded tree: (1) species; (2) diameter at 1.4 m above ground (DBH); (3) distance to river edge (high water mark); (4) number of wounds per tree; (5) wound length, width, and depth; (6) wound age; (7) wound orientation; (8) percentage of tree circumference wounded; and (9) presence of altered wood behind wound. Wound size (area) was calculated by multiplying wound length and width by 0.75 ($L \times W \times 0.75$) to compensate for elliptical wound shape. Wound age was determined with an increment borer by counting annual rings between scar tissue and bark on extracted cores. Altered wood was detected with an increment borer by examining cores for discolored or decayed wood.

Results and Discussion

A total of 160 wounds on 148 trees were examined in three locations along the Grande Ronde River in Union County, Oregon. Trees ranged in size from 7.9 to 128.5 cm in DBH and were 0 to 65.8 m from the river edge. Wounds were examined principally on black cottonwood (*Populus trichocarpa* Torr. and Gray), ponderosa pine

(*Pinus ponderosa* Dougl. ex Laws.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and willow (*Salix* spp.) with some observations on lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and black locust (*Robinia pseudoacacia* L.). No species appeared resistant to wounding. In all cases, wounds were on the up-river side of the tree and less than 1.6 m above the ground (Figure 1). In some cases, wounds were extremely large (14,066 cm²) and deep (6.5 cm) and completely girdled stems resulting in tree mortality. In all cases, both outer and inner bark were removed by ice movement. Trees as far as 65 m from the river edge were wounded, testifying to the extreme lateral movement of ice.

Some incipient decay was detected in a few cottonwoods. Wood in most trees still appeared healthy behind the wounds. Most wounds resulting from an ice flow in January 1984 were only two years old, however; this may not have been sufficient time to allow development of advanced decay in wounded cottonwoods, a normally decay-prone species. Two ponderosa pines at

one site each had two and three major wounds that were about 2, 20, and 50 years old. No decay was associated with these wounds. Based on these data, it seems that mass ice movement causing tree wounding may be a 20- to 30-year event along portions of the Grande Ronde River and possibly other rivers in eastern Oregon and Washington.

Besides predisposing trees to stem decay and failure within developed recreation sites, mass ice movement also may alter wildlife habitat by damaging vegetation within riparian zones. Trees and shrubs in riparian zones provide cover, nesting, and feeding opportunities for wildlife and thermal cover to regulate water temperature for fish (Thomas *et al.* 1979). In our study on the Grande Ronde River, we examined shrubs at the study sites and along major tributaries of the Grande Ronde River and found that some shrubs had been killed directly by mass ice movement that removed large sections of bark or broke stems (Figure 2). In addition, dead and dying mountain alder (*Alnus incana* (L.) Moench), a dominant plant species along watercourses in



Figure 1. Stem wounds on ponderosa pine trees caused by mass ice movement. All wounds are on the up-river side of the tree and less than 1.6 m above the ground.



Figure 2. Mountain alder along the Grande Ronde River killed by mass ice movement.

Oregon and Washington, had cankers associated with a fungus identified as *Cytospora* sp. (Filip, unpublished). The genus *Cytospora* is a saprophyte or weak parasite of many hardwoods and conifers in North America (Scharpf 1969, Partridge 1976, Funk 1981). Living stems usually need to be weakened or wounded for fungal infection and canker formation. We hypothesized that the mass ice movement may be contributing to the decline of the alder by directly killing stems and by providing a food base and subsequent inoculum source for *Cytospora* to infect

living stems wounded superficially by floating ice sheets. Stem wounding is usually required for infection by *Cytospora*, and other tree and shrub species growing with alder, such as black hawthorn (*Crataegus douglasii* Lindl.) and red-osier dogwood (*Cornus stolonifera* Michx.), are not affected by *Cytospora* (Filip, unpublished.)

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Cattle Grazing Effects on Understory Cover and Tree Growth in Mixed Conifer Clearcuts

Abstract

A long-term study of cattle grazing effects on shrub and herbaceous cover and tree growth in mixed conifer clearcuts began at Blodgett Forest Research Station on the west slope of the Sierra Nevada in 1977. Until that time, no studies had quantified the relationships between cattle grazing and reduction in non-tree vegetation, and grazing damage to tree regeneration. Yet, with the ban on use of herbicides in Federal forest management, alternative tools for reducing unwanted vegetation were needed. Cattle grazing reduced shrub and herbaceous canopy cover to 8 percent six years after harvesting, and 31 percent eight years after harvesting on two mixed conifer clearcuts. These cover levels were within timber management objectives for tree growth. No significant trampling damage occurred and browsing damage to white and Douglas-fir seedlings was primarily caused by deer. Tree seedlings showed no significant differences in height or basal diameter growth under any treatment. Thus, cattle grazing appears to be a viable tool for meeting brush/grass objectives in forest plantations.

Introduction

Domestic livestock have grazed western forest ranges since the mid-1800's. Forest ecosystems provide high quality summer forage commonly unavailable at lower elevations, ample water, and relative freedom from insects and disease. Large numbers of livestock began to use California's forest ranges and mountain pastures as a local market for red meat emerged following the discovery of gold and increases in human settlement in the 1850's (Burcham 1981, Kosco and Bartolome 1981). In 1986, 497,000 AUMs (animal unit months) of livestock grazing were permitted on U.S. Forest Service administered land in California. At the same time, California forest ecosystems also provided 3.4 billion board feet of timber, 100 million recreation visitor days, 50 million acre-feet of water and primary wildlife habitat for some 311 vertebrate species (Ewing *et al.* 1988).

Foresters have expressed concern over livestock damage to young conifer plantations since the turn of the century (Jardine and Anderson 1919). Examples of the conflicts between livestock grazing and intensive timber management are numerous, with tree seedling damage figures varying between 25 percent browsing damage (Kosco and Bartolome 1983) and severe damage to tree regeneration (Arvola 1978). Early research emphasized that browsing and trampling damage to plantations resulted from faulty livestock management, not inherent incompatibility of grazing and reforestation (Jardine and Anderson 1919, Cassidy 1937, Heerwagen 1954). For exam-

ple, research on Weyerhaeuser Corporation lands in southeastern Oregon suggested that proper timing of cattle grazing is essential for successful plantation management (Fulgham 1985). Although many foresters continue to believe grazing and timber production do not mix, livestock continue to be an important multiple-use of forest ecosystems.

The 1978 ban on the use of herbicides in California USFS timber management stimulated several research projects to specifically evaluate livestock grazing in tree plantations. Several research projects have now documented that livestock grazing and intensive forest management need not conflict, and indeed may be mutually beneficial by reducing competition to tree seedlings and providing forage for livestock (e.g. Kosco 1980, Kosco and Bartolome 1983, Monfore 1986, Thomas 1983).

Shrub and herbaceous species growth on plantations following timber harvesting is estimated to reduce timber volumes by up to 30 percent (USFS 1986). Shrub volumes of 10,000 cubic feet (Bentley 1971) or canopy cover over 30 percent (Fiske 1981) appear to be sufficient to reduce conifer volume growth. Although some evidence suggests that shrubs may aid initial conifer survival without impairment of early height growth (Roy 1981), subsequent loss of volume growth from competing brush species is significant. Grass competition with young conifers appears to be even more detrimental to conifer volume production than brush on many sites (USFS 1986).

A few research studies now indicate the potential, problems, and some solutions for plantation grazing. Research on Weyerhaeuser Corporation land in Oregon indicated that tree browsing damage was directly related to starting date of grazing (Monfore 1983). Knowledge of seasonal forage palatability has resulted in better livestock management to meet timber management objectives and protect sensitive riparian areas on Weyerhaeuser lands. Sharrow and Leininger (1982) reported that tree damage from sheep was confined to early spring and that key browse species could be used to define the proper grazing season for effective plantation management.

Our central hypothesis was that coordinated cattle grazing can keep competing, unwanted vegetation at acceptably low levels without significant damage to conifer regeneration in mixed conifer clearcuts. The objectives of this study were to: (1) measure long-term brush and herbaceous cover changes following clearcutting with and without grazing by cattle and deer, (2) evaluate the effects of cattle browsing and trampling damage on conifer regeneration, and (3) examine the effect of brush canopy cover on tree seedling height and basal diameter growth. Results through 1980 summarizing the first two years of research were reported earlier (Kosco 1980, Kosco and Bartolome 1983). This paper summarizes results after six and eight years for two clearcuts and integrates the results into management suggested guidelines.

Methods

Blodgett Forest Research Station (BFRS) is located near Georgetown, California in the mixed conifer forest zone on the west slope of the Sierra Nevada at about 1300-1500 m elevation. It is owned and managed by the Department of Forestry and Resource Management at University of California, Berkeley and has operated as a natural resources research station since the 1950's.

BFRS comprises 1250 ha divided into approximately 65 distinct forest management units. Topography is varied, but slopes of > 50 percent are uncommon (Kosco 1980). Four distinct soil series occur on BFRS (Zinke *et al.* 1965). Three soil series, Musick, Holland, and Chanwanakee, are derived from granodiorite and average 1.5 m

deep. The fourth series, Windy, is derived from andesite parent material which tends to be less weathered, though numerous fissures allow root penetration.

The study area has a Mediterranean climate with relatively dry, hot summers and mild, wet winters. Long-term precipitation averaged 157.5 cm per year, with an average frost-free period of 172 days, generally May through October (BFRS unpublished records on file). Snow commonly occurs from November through February (Kosco 1980).

Cattle graze the southern 600 ha of BFRS each year from approximately 30 May until 1 October. The 35 animal units are free-roaming, with mature cows familiar with the forest range and yearling heifers turned out together in groups of eight to ten. Water is abundant and well-distributed over the station. Small stringer meadows and patches of browse, primarily deerbrush (*Ceanothus integrifolius*) provide locally abundant, high quality, palatable forage.

Two clearcuts on the grazed portion of the BFRS were chosen for detailed study because of their availability, and similarities in physical site characteristics, clearcut harvesting techniques employed, and expected understory vegetation response. Both units were cut as part of the normal BFRS timber harvesting program using standard harvesting procedures for mixed conifer forests.

Clearcut 481 is 8.1 ha on a 30 percent, east-facing slope. The unit was harvested in August 1975 and prepared for planting using a D-4 crawler tractor equipped with a brush rake to pile brush in August 1976. Harvest residue piles were burned that fall. In April 1977 the clearcut was planted to 1-0 ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*P. lambertiana* Dougl.), Douglas-fir (*Pseudotsuga menziesii* Lamb.) and 2-0 white fir (*Abies concolor* Lindl. & Gord.). Forty 2.5 x 2.5-m plots, twenty grazed and twenty ungrazed plots, were randomly located in pairs on the clearcut using a grid overlay and random coordinates in 1978. Pre-established rules for plot location ensured that plots would not be placed within 10 m of the clearcut boundary, that the first planted tree seedling to the north of the random location point would be in the plot, and the grazed plot of the pair would be systematically located 3 m to the north of the exclosed plot.

Exclosures made of 2-m tall woven, 10 x 10-cm mesh wire prevented grazing by both cattle and deer.

Clearcut 321 is a 6 ha clearcut on a site similar to Clearcut 481. The clearcut was harvested in June 1980 and prepared for planting using a D-4 tractor equipped with a brush rake to pile slash and brush in August 1980. Harvest residue piles were burned in the winter of 1980-81. The unit was planted to a mixture of 1-0 and 2-0 ponderosa pine, white fir, Douglas-fir and giant sequoia (*Sequoiadendron gigantea* Lindl.) the following April. Sixteen areas were randomly located on the clearcut in 1981 for placement of sets of four 3 x 3-m plots using the same procedures used on Clearcut 481. Four treatments were tested: no grazing, grazing by deer alone, grazing by cattle and deer, and removal of all non-tree vegetation by clipping. Plots grazed by deer alone were fenced with cattle-proof barbed-wire which allowed access by deer. Exclosures were established the same year as tree planting and prior to that season's cattle grazing.

All vegetation measurements were collected in early fall at the end of the livestock grazing season and before the main deer migration season began. Herbaceous and shrub canopy cover, by species, was ocularly estimated on all treatments on both clearcuts by the same person in all years. Data for tree seedlings, measured height to the nearest centimeter, basal diameter at ground level to the nearest millimeter, and any apparent browsing and trampling damage, were recorded for each tree seedling on the treatment plots. The clipped treatment on Clearcut 321 was sampled as above and subsequently clipped to remove all aboveground biomass annually. Data were collected annually (1981-1986) on Clearcut 321 and in 1979 and 1984 on Clearcut 481.

Means and 95 percent confidence intervals were used to compare differences in shrub/herbaceous cover by treatment using Student's *t* (Zar 1984). One-way and two-way analysis of variance were also used to test significant differences in tree heights and basal diameters between treatments. Means were separated using Duncan's New Multiple Range test. Plots were used as blocks in the two-way ANOVA, to see if the plots themselves explained the tree variation. Analysis of covariance was used to determine if tree heights were systematically associated with

shrub covers in the plots. Values for browsed tree seedlings were compared using the binomial distribution.

Results and Discussion

Seventeen shrub and herbaceous species were present on Clearcut 321 in 1986. Deerbrush, gooseberries (*Ribes roezli* Regel), greenleaf manzanita (*Arctostaphylos patula* Greene), and bull thistle (*Cirsium vulgare* Savi.) were the most frequent species occurring in 16, 16, 13 and 12 sample plots, respectively. Deerbrush contributed the greatest non-tree canopy cover on the clearcut. Herbaceous species were relatively uncommon (Table 1). Mean canopy cover of deerbrush in 1986 was less ($p < 0.05$) on grazed plots than ungrazed or plots grazed by deer only, averaging 1 percent, 52 percent and 20 percent respectively. Gooseberries and greenleaf manzanita

TABLE 1. List of shrub and herbaceous species encountered on Clearcuts 481 and 321. Value is frequency of occurrence. All plant species names are from Munz and Keck (1973).

Plant Species	Clearcut 321 (n = 16 plots)	Clearcut 481 (n = 20 plots)
Shrubs		
<i>Ceanothus integerrimus</i>	15	15
<i>Ribes roezli</i>	15	2
<i>Arctostaphylos patula</i>	13	16
<i>Lithocarpus densiflora</i>	6	—
<i>Rosa pinetorum</i>	3	1
<i>Quercus kelloggii</i>	2	5
<i>Prunus emarginata</i>	2	—
<i>Symphoricarpos acutus</i>	2	—
<i>Corylus cornuta</i>	2	—
<i>Rubus parviflorus</i>	2	—
<i>Chamaebatia foliolosa</i>	1	8
<i>Baccharis pilularis</i>	1	—
<i>Ceanothus cordulatus</i>	—	1
Herbs		
<i>Cirsium vulgare</i>	12	8
<i>Carex</i> spp.	5	1
<i>Tridentalis europaea</i>	4	—
<i>Trifolium</i> spp.	3	—
<i>Stipa lettermanii</i>	2	1
<i>Lactuca seriola</i>	2	—
<i>Verbascum thapsus</i>	1	1
<i>Galium aparine</i>	1	—
<i>Epilobium</i> spp.	1	—
<i>Pyrola picta</i>	1	—
<i>Dicentra uniflora</i>	1	—
<i>Agoseris</i> spp.	1	—
<i>Bromus marginatus</i>	—	1
<i>Iris Hartwegii</i>	—	1

occurred in similar amounts on the grazed, ungrazed and deer-grazed treatments. Bull thistle was found more often on deer grazed and grazed plots.

Total shrub and herbaceous canopy cover was reduced by grazing in Clearcut 321 (Figure 1). Canopy cover by treatment differed ($p < 0.05$) between all treatments in all years except 1983. Total canopy cover increased on Clearcut 321 from the time of harvesting until 1985. In 1986, canopy cover declined on all treatment plots indicating the onset of tree dominance and the beginning of full site occupancy. Grazed plots continued to have less herbaceous and shrub canopy cover than ungrazed plots, and plots grazed by cattle and deer continued to have less cover than plots grazed by deer alone.

Fourteen plant species were present on Clearcut 481. Deerbrush, squaw carpet (*Ceanothus prostratus* Benth.), greenleaf manzanita, bull thistle and gooseberries were the most common species, reflecting the pre-harvest species composition

(Table 1). Although total canopy cover increased on grazed and ungrazed treatments (Figure 2), grazed plots had less shrub and herbaceous canopy cover (31%) than ungrazed (75%) plots.

Cattle grazing, in combination with transitory deer use, decreased shrub canopy cover to 8 percent on Clearcut 321 six years after harvesting and 31 percent on Clearcut 481 eight years after harvesting. These shrub levels are within the BFRS timber management recommended allowable brush levels to meet tree growth and timber management objectives (R. C. Heald, pers. communication).

On all grazed plots on Clearcut 321, white fir and Douglas-fir were the only species browsed, at 17 percent and 33 percent respectively (Table 2). Browsing on small trees averaged 10 percent overall on Clearcut 321, while only 1 white fir was browsed on Clearcut 481. We believe that the browsing or trampling damage to tree seedlings was insignificant to affect timber management goals on either clearcut.

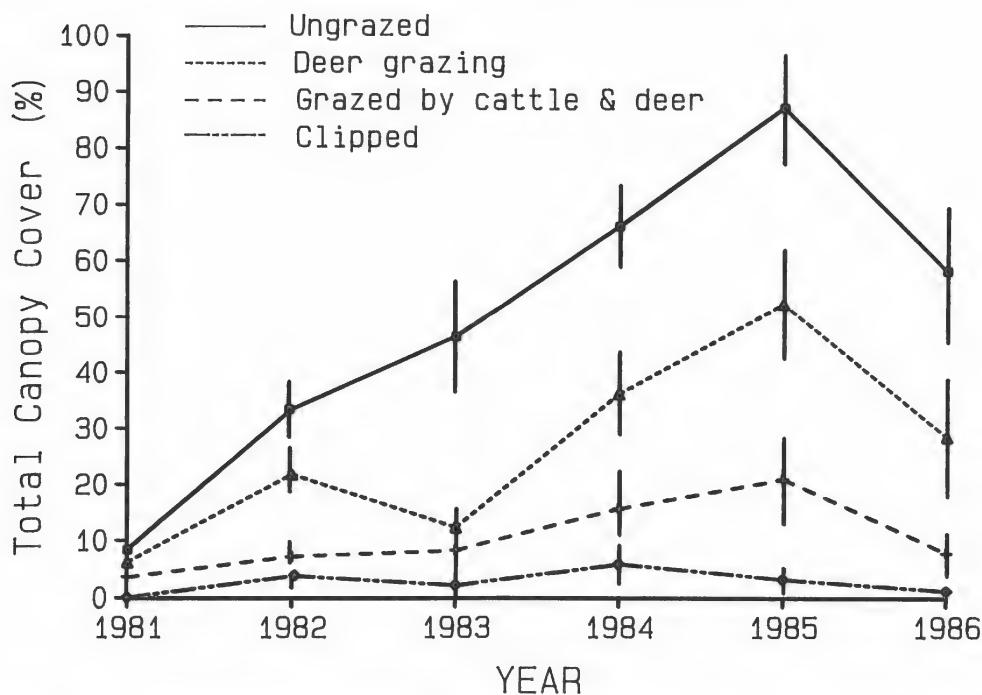


Figure 1. Changes in total shrub and herbaceous canopy cover on Clearcut 321 following tree planting. Values are means from twenty 2.5 x 2.5-m quadrats with 95% confidence bands. The site was harvested in June 1980, prepared for planting in August 1980, burned in the winter of 1981 and planted in spring 1981.

TABLE 2. Number of tree seedlings browsed by species and treatment in treatment plots on Clearcut 321. Data were collected in September 1986.

Treatment	WHITE FIR		DOUGLAS-FIR	
	No. Browsed	Total No.	No. Browsed	Total No.
Ungrazed	0	25	0	0
Grazed	6 ^a	24	1 _b	4
Deer Grazed	5 ^a	21	0	0
Clipped	4 ^a	17	2 ^b	6
Total	15	87	3	10

Superscript of the same letter means that the values are not significantly different using the binomial distribution.

No significant differences in tree height or basal diameter growth were found between treatments on either clearcut (Table 3). Also, comparing individual species' heights and basal diameters of all tree species combined with shrub and herbaceous canopy cover on a plot by plot basis did not reveal significant relationships

TABLE 3. Average height (cm) and basal diameter (cm) of all trees by treatment on Clearcut 321 (4 years after planting) and Clearcut 481 (8 years after planting). No significant differences were found in tree height or basal diameter, collectively or individually, by treatment. Standard deviation is given in parentheses. Tree sample size equals 18 instead of 20 on Clearcut 481 because of inadvertent tree removal on two plots.

Treatment	Clearcut 321 (n = 16)		Clearcut 481 (n = 18)	
	Height	Basal Diameter	Height	Basal Diameter
Ungrazed	43.3 ^a (12.4)	0.6 (0.2)	102.3 ^b (30.8)	1.0 (0.3)
Grazed	45.3 ^a (19.2)	0.6 (0.3)	89.8 ^b (23.3)	1.1 (0.3)
Deer Grazed	41.3 ^a (13.9)	0.5 (0.2)		
Clipped	52.4 ^a (26.5)	0.8 (0.3)		

Superscript of the same letter indicates that the means are not significantly different using Duncan's New Multiple Range test.

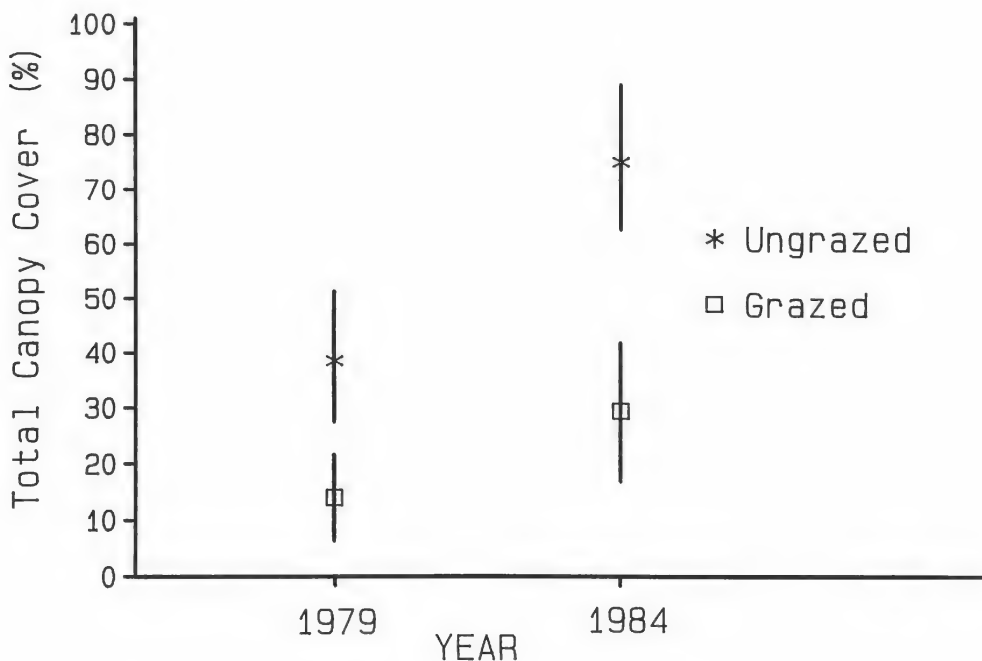


Figure 2. Changes in total shrub and herbaceous canopy cover on Clearcut 481 following tree planting. The site was harvested in August 1975, prepared for planting in August 1976 and planted in April 1977.

between tree height or basal diameter and shrub and herbaceous cover. The lack of difference in tree height or basal diameter by treatment could be a result of several factors. The study design used small exclosures to examine the main variables of shrub and herbaceous canopy cover and browsing damage; however, the plots are smaller than the area now occupied by a tree, so that differences in treatment are unlikely to affect many trees. Future differences in tree growth may occur, but inter-tree competition now confounds potential effects.

Conclusions

Cattle grazing can be used to reduce herbaceous and shrub canopy cover on clearcuts with no detrimental impact on tree seedlings. We believe, however, that successful application of this tool requires more advanced planning and coordination than other vegetation management techniques. For example, the potential post-harvest forage mix is critical to attract cattle to clearcuts (Kosco and Bartolome 1983). If suitable forage species are not present, cattle grazing management for brush control will be ineffective.

Land managers need to carefully examine a site to determine if livestock will effectively use the area. Sheep may effectively graze greater slopes (up to 60%) than cattle (generally up to 50%), but topography, slope, aspect, distance from water and access will all affect animal use (Heady 1975). Cattle on BFRS have plentiful, well-distributed water and gentle slopes making all parts of BFRS potentially available for cattle grazing. Areas without well-distributed water or with steep topography would require water developments to make effective use of plantation vegetation.

Our experience comparing cattle and deer browsing indicates that managers must identify the potential causes of damage to conifer seedlings and develop a plan to verify damage source(s) if it occurs. This planning should also initiate a discussion of what percent mortality is acceptable. Some tree browsing and/or trampling damage will occur even under the best livestock

management, yet browsing damage from livestock grazing may have negligible economic impact (Thomas 1985, Heald 1986). Grazing plantations with livestock when shrubs or herbs are more palatable than tree seedlings results in little damage to trees (Fulgham 1985, Sharrow and Leininger 1982, Monfore 1983). In fact, deer, elk, and rodents often cause most of the browsing damage to young plantation conifers (Kosco and Bartolome 1983, Kingery *et al.* 1987, G. Fiddler pers. communication).

Finally, it should be noted that even though our study did not indicate that significant reductions in shrub canopy cover would result in greater tree growth, we believe that shrubs *do* compete with conifers for moisture and light. We hypothesize that the small ungrazed plot size used in this study, coupled with the reduction in shrub canopy cover on the clearcuts as a whole, masked the localized shrub effect on tree growth. We suggest that any methods to reduce shrub canopy cover that are economical, environmentally sound, and meet management objectives should be available to timber managers (Fiddler and McDonald 1986). Researchers need to provide more detailed information on the relationships between tree, shrub and grass growth for many species and site conditions.

Coordinated cattle grazing has effectively reduced shrub canopy cover on two clearcuts at BFRS with little damage to tree regeneration, provided an annual income to the forest property, and aided the forest manager in meeting timber management objectives. With advanced planning and understanding of forest/forage relationships, livestock may become a more important forest management tool in the future.

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Biomass Regression Equations for Determination of Vertical Structure of Major Understory Species of Southeast Alaska¹

Abstract

Describing structural aspects of forest vegetation is now routine in forest inventories in Alaska. The biomass structure of understory vegetation is considered a necessary part of the inventory process. In this study twig, foliar and combined (twig plus foliar) biomass were related to percent cover for 48 species common to southeast Alaska. Biomass values calculated with these equations yield estimates of kilograms biomass per hectare for a 10 cm vertical layer. Thus a vertical understory biomass profile can be estimated utilizing these equations and an appropriate set of cover estimates. A destructive sampling technique was used to estimate understory biomass and was compared to an estimate derived from a nondestructive application of the derived regression equations. The nondestructive estimate fell within the 95% confidence limits of the biomass estimate derived from the destructive sample. This indicates that the regression approach will result in estimates of understory biomass in vertical layers with similar accuracy as the more costly and time consuming harvest technique.

Introduction

Describing the structure of forest vegetation is now a routine part of many forest inventories (Cost and McClure 1982a, 1982b, McClure *et al.* 1979, O'Brien and Van Hooser 1983, LaBau and Schreuder 1983, Larson and Mead 1983). Use of this type of information for biomass estimates, crown fuel estimates, measures of forest diversity, and environmental assessment have been suggested (Cost 1979). Vegetation structure can also be used to assess wildlife habitat (Cost 1979) and to analyze the validity of vegetation classification systems (Smith and Larson 1984). Profiles of understory twig and leaf biomass have been shown to be useful in estimating the distribution and abundance of honeysuckle (*Lonicera spp.*) in South Carolina (Craver 1982). The estimates of biomass can be used when forage quantities are needed to ascertain wildlife carrying capacity or quality of habitat.

The USDA, Pacific Northwest Experiment Station, Forest Inventory and Analysis Unit, Anchorage, Alaska, has been collecting data to describe forest structure for the past five years in multiresource inventories in both interior and southeastern Alaska. Estimates of percent cover based on vertical stratification are a routine part of the data collection methods of the multi-

resource inventories performed within Alaska. The extension of these cover estimates to biomass profiles requires the development of equations to estimate biomass based on percent cover within defined vertical strata. These estimates differ from conventional equations used to estimate biomass (see Alaback 1986) in that the vertical extent of the vegetation sample is controlled (Yarie and Mead 1988).

The objectives of this study were to: 1) develop equations to predict twig and foliar biomass from estimates of percent cover within defined vertical segments through a 2.5 meter vertical profile of understory vegetation in southeast Alaska; and 2) to compare destructive estimates, based on harvested vegetation, of biomass structure to those obtained using the nondestructive percent cover-biomass equations with estimates of percent cover by vertical layers.

Methods

Site Selection

A total of 20 sites was used for destructive sampling to develop the regression equations. The sites were selected to represent the major level IV vegetation types (Vioreck *et al.* 1986) encountered during the renewable resource inventory of southeast Alaska (Table 1). The sites ranged from closed forest at sea level to open coniferous forests close to timber line. This wide

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range was considered necessary in order to sample and develop regression equations for as many species as possible. Biomass samples were taken during 1985 and 1986 throughout the summer periods (15 June through 31 August). Alaback (1986) has shown that the length of this sample period does not significantly affect biomass regression estimates.

Regression Equation Development

Field sampling was carried out using a technique similar to that of Harcombe and Marks (1977). A vertical profile was delineated in 1985 by suspending ropes from an aluminum frame attached to a 14 foot stepladder. In 1986, the profile was defined by constructing a free standing frame from 1/2" CPVC pipe. Segments were marked on the vertical pipe or rope every 0.3 meters. The sampling frame extended to 2.5 meters above the ground surface. Percent cover was visually estimated by species for each 0.3 meter vertical segment of the 0.56 square meter plot (2 feet x 3 feet) starting at the highest level in which vegetation occupied the sample volume. The sample was then clipped and returned to the lab for drying at 65°C and weighing to the nearest 0.01 grams. Shrub samples were separated into leaves and twigs less than five millimeters in diameter prior to drying. Field sampling began by estimating percent cover for each species in the highest layer, after which that layer was clipped. This method was followed for each successive layer down to the ground. A maximum of ten sample plots (range 2 to 10) was located at each site. The exact number was determined by availability of transportation to each site and the complexity of the vegetation at the site.

Statistical Analysis

A conditioned regression was used to define the relationship between percent cover and biomass for each species. The form of the equation is:

$$y = aC$$

where y = measured biomass (Kg/ha layer) of leaves, twigs or total (twigs + leaves)
 C = estimated cover (percent)
 a = regression coefficient

A dummy variable analysis was used to test for differences between the slope of equations for different layers within a vegetation type, and then between vegetation types for layers or groups of

layers that were found to be similar within vegetation types. An F-test was used to test the equality of regression slopes from equations developed in different years.

Horizontal-Vertical Profile (Destructive Biomass Sample)

The horizontal-vertical profile (H-V) plot (McClure *et al.* 1979) was used to define the horizontal and vertical distribution and density of the vegetation (within a circular 100 square meter plot). The distribution of vegetation in each H-V plot was measured using the space occupancy concept (McClure *et al.* 1979). The vegetation was classified by layers. The first layer was at ground level. The remaining layers were determined using the natural breaks in vegetation distribution up to a maximum height of 5 meters. For each layer the vertical height of the foliage was recorded to the nearest decimeter.

The total percent cover of all species for each layer was estimated. Then the percent occupancy (percent of the total cover of a layer contributed by a single species; the sum of the percent occupancy values is always 100% for any layer) of each species was estimated. The percent cover of each species can then be estimated by multiplying the proportional occupancy by the total percent cover for the layer. For example if two species are present in one layer which has a total cover of 70 percent, and species A represents 40 percent of the layer and species B represents 60 percent of the layer then the percent cover of species A is 28 percent ($0.4 \times 70\%$).

Twig and foliar biomass was estimated using a destructive clip plot technique in one H-V plot on sites JUN078, MTF167 and STK114 (Table 1). Ten subplots split equally were sampled within each circular H-V plot along two perpendicular diameters. Prior to destructive sampling Forest Service personnel estimated the percent cover by species in the H-V plot. These biomass data were initially used to compare the regression estimates of biomass to destructively sampled estimates for individual sites. After this analysis was completed the two data sets were merged to develop the equations presented in this paper. Sets of 95 percent confidence limits were calculated around the total twig and foliar biomass destructively estimated for each H-V plot. These were compared with the nondestructive biomass estimate

obtained by applying the biomass equations with the estimated percent cover in the H-V plot. The vertical biomass structures of the H-V plot estimated using the destructive and nondestructive techniques were compared graphically due to the differences in the methods of determining individual layers.

Results and Discussion

Biomass Equations

Significant regressions were developed for 48 species typical of southeast Alaska (Table 2). In order to provide the broadest species coverage, species with as few as ten observations are included in the table with the exception of *Calamagrostis* spp. and *Streptopus roseus*. A better representation of the natural variability would be achieved with a sample size of 30 or greater spread over several vegetation types. Over 70 percent of the regression equations presented had an r^2 greater than 0.7 (range .41 to .99; Table 2). The maximum percent cover sampled is presented in Table 2. The minimum was always zero.

The equations represent total biomass (Kg/ha) of species that occupy the ground layer (layer 0) or the first vertical segment (layer 1) and that never have stems larger than 5 mm in diameter.

All other equations predict biomass in kilograms for a layer that is 10 cm high. Total biomass is calculated by estimating the biomass for each layer and then summing all layers. Also because the equations yield a biomass estimate based on a hectare of surface area it is important that the percent cover estimate used be representative of a large area. Alaback (1986) presents a detailed analysis of plot size and numbers of plots necessary to obtain a good estimate of understory biomass in southeast Alaska.

The equations presented in Table 2 were developed with the assumption that there were no differences in coefficients between different vertical strata or community types. This assumption was not true for all species (Table 3 and 4) although very few layer and vegetation differences were found in this study or for vegetation in interior Alaska (Yarie and Mead 1988).

Significantly different coefficients representative of different vegetation types were found for nine of the species sampled (Table 3). The revised equations presented in Table 3 show a reduction in the standard error of estimate if the vegetation type is known. For example, the standard error of estimate decreased from 41.59 to 13.68 for *Hylocomium splendens* while the standard error of estimate for stem weight of *Vaccinium*

TABLE 1. Site location and vegetation type for areas selected for development of biomass equations.

Gen. Location or USFS Inventory Plot	Elevation (m)	Slope (%)	Aspect (degrees)	Level IV Vegetation Type (Viereck <i>et al.</i> 1986)	
JUN078	30	3	flat	1A1B	Closed western hemlock
Naukati Bay	30	—	flat	1A1D	Closed western hemlock-Sitka spruce-western redcedar
	30	—	flat	1A1C	Closed western hemlock-Sitka spruce
	60	—	flat	1A1B	Closed western hemlock
	30	—	flat	1A1A	Closed Sitka spruce
PTB052	122	10	90	1A2X	Open mixed softwoods
PTB108	183	10	200	1A2X	Open mixed softwoods
CRG025	122	22	90	1A1C	Closed western hemlock-Sitka spruce
CRG095	30	45	310	1A1D	Closed western hemlock-Sitka spruce-western redcedar
CRG021	335	25	250	1A1E	Western hemlock-yellow cedar
PTB056	183	10	11	1A1X	Closed mixed conifer
PTB082	549	35	33	1A1G	Closed western hemlock-western redcedar
Sitka	30	—	flat	1B1B	Closed black cottonwood
STK054	396	73	10	1A1G	Closed western hemlock-western redcedar
STK054	396	73	10	1A3X	Undescribed coniferous woodland
MTF167	30	19	140	1A1X	Undescribed closed mixed conifer
Sitka	30	1	flat	1D3A	Muskeg
Sitka	30	1	flat	2B1X	Undescribed closed tall shrub (<i>Rubus</i>)
STK114	30	1	flat	1A1A	Closed Sitka spruce
Harbor Mt	670	60	345	1A2E	Open white spruce

TABLE 2. Equations for predicting biomass (kg/ha) for a 10 cm high vertical layer of common understory species found in southeast Alaska. The form of the equation is $y(\text{kg/ha})$ for a 10 cm vertical layer = $a \cdot \text{percent cover}$.

Species ¹	Layers Sampled	No. of Plots	Regression Coefficient(a)	r ²	Std Err of Estimate	% Cover Maximum	Vegetation types Sampled ²
Mosses							
<i>Dicranum sp.</i>		25	4.050	0.78	9.27	12	1A1B, 1A1C, 1A1D, 1A1G, 1A1X
<i>Hylocomium splendens</i>		85	3.692	0.67	41.59	90	1A1A, 1A1B, 1A1C, 1A1D, 1A1E, 1A1X, 1A2X
<i>Mnium sp.</i>		29	4.524	0.88	3.31	8	1A1A, 1A1B, 1A1C, 1A1D, 1A1G, 1A2X
<i>Rhytidiadelphus loreus</i>		13	5.223	0.90	90.58	100	1A1A, 1A1X
<i>Rhytidiadelphus sp.</i>		64	5.456	0.99	2.56	20	1A1A, 1A1B, 1A1C, 1A1D, 1A1E, 1A1G, 1A1X, 1A2X
<i>Sphagnum sp.</i>		30	3.534	0.70	65.20	95	1A1B, 1A1C, 1A1E, 1A1G, 1A1X, 1A2X
Lichens and Liverworts							
<i>Hepaticae</i>		29	0.291	0.69	4.83	95	1A1A, 1A1B, 1A1C, 1A1D, 1A1G, 1A1X
Ferns							
<i>Athyrium sp.</i> lady fern	1-5	21	2.660	0.93	14.66	65	1A1A, 1A1B, 1A1C
<i>Blechnum spicant</i> deer fern	1-3	14	5.588	0.87	30.48	35	1A1A, 1A1C, 1A1D, 1A1G, 1A1X, 1A2X
<i>Dryopteris dilatata</i> Spinulose shield fern	1	30	2.069	0.57	14.22	15	1A1A, 1A1B, 1A1G, 1A1X
<i>Gymnocarpium dryopteris</i> oak fern	1	40	0.821	0.79	9.23	70	1A1A, 1A1B, 1A1C, 1A1D, 1A1X
Grass and Grasslike							
<i>Calamagrostis spp.</i> reed bentgrass	1-4	8	1.214	0.91	7.66	40	1B1B
<i>Carex sp.</i>	1	35	1.336	0.82	32.12	50	1D3A
Grass & Grass like	1	22	2.155	0.66	70.72	100	1A1A, 1A1G, 1A1X, 1A2B
<i>Trichophorum caespitosum</i> trufted clubrush	1	11	2.292	0.83	26.74	45	1D3A
Forbs and Low Shrubs							
<i>Cassiope mertensiana</i> Mertens cassiope	1	14	21.325	0.95	213.53	98	1A1G, 1A2E, 1A3X
<i>Cassiope stellariana</i> Alaska moss heath	1	13	4.613	0.82	133.88	95	1A1G, 1A2E, 1A3X
<i>Coptis asplenifolia</i>	1	40	0.866	0.48	16.04	3	1A1B, 1A1C, 1A1D, 1A2E, 1A1X, 1A2X
<i>Cornus canadensis</i> bunchberry	1	63	0.838	0.52	14.05	60	1A1G, 1A1C, 1A1D, 1A1E, 1A1X, 1D3A
<i>Empetrum nigrum</i> black crowberry	1	11	5.850	0.94	77.17	90	1A1G, 1A2E
<i>Erigeron spp.</i> fleabane	1	10	0.652	0.91	1.86	17	1A1G, 1A1X, 1A2E, 1A3X
<i>Fauria crista-galli</i> deer cabbage	1-2	22	1.933	0.95	25.69	97	1D3A
<i>Gentiana douglasiana</i> swamp genetain	1	10	1.865	0.68	1.52	2	1A1X, 1D3A
<i>Luetkea pectinata</i> luetkea	1	13	1.156	0.76	29.60	75	1A1G, 1A2E, 1A3X

TABLE 2 (Cont.)

Species ¹		Layers Sampled	No. of Plots	Regression Coefficient(a)	r ²	Std Err of Estimate	% Cover Maximum	Vegetation types Sampled ²
Forbs and Low Shrubs								
<i>Lysichiton americanum</i>		1-3	35	3.597	0.58	72.89	65	1A1B, 1A1C, 1A1E, 1A1X,
yellow skunk cabbage								1A2X
<i>Maianthemum dilatatum</i>		1	11	1.460	0.90	29.14	95	1A1A, 1A1B, 1A1X, 1B1B
deerberry								
<i>Rubus pedatus</i>		0	49	0.495	0.75	2.35	55	1A1A, 1A1B, 1A1C, 1A1E
five-leaf bramble								
<i>Streptopus amplexifolius</i>		1-2	10	0.754	0.82	4.53	30	1A1G, 1A1X, 1A2X, 1A2E,
twisted stalk								1A1A, 1A1G, 1A1X, 1B1B
<i>Streptopus roseus</i>		1	9	1.515	0.97	9.26	96	1A1B, 1A1C, 1A1G, 1A2E
simple stem twisted stalk								
<i>Tiarella trifoliata</i>		1	24	0.527	0.41	2.72	15	1A1A, 1A1B, 1A1C, 1A1G,
three leaf lace flower								1A1X, 1A2X, 1B1B
<i>Veratrum viride</i>		1-2	15	3.452	0.89	18.73	40	1A1A, 1A1G
false hellebore								
<i>Viola sp.</i>		1	10	0.648	0.75	3.49	17	1A1A, 1A1X, 1B1B
Violet								
Mid-Sized Shrubs								
<i>Gaultheria shallon</i>	TOTAL	1-2	17	11.534	0.91	138.72	75	1A1D, 1A2X
Salal	LEAF		17	6.349	0.95	56.03		
	STEM		17	5.184	0.71	125.43		
<i>Kalmia polifolia</i>	TOTAL	1	11	4.481	0.94	6.97	11	1D3A
bog laurel	LEAF		11	2.174	0.90	4.29		
	STEM		11	2.307	0.93	3.77		
<i>Ledum groenlandicum</i>	TOTAL	1	11	3.551	0.80	17.32	15	1D3A
labrador-tea	LEAF		11	1.891	0.83	8.28		
	STEM		11	1.660	0.75	9.46		
<i>Vaccinium caespitosum</i>	TOTAL	1	11	2.616	0.90	49.93	95	1A2E
dwarf blueberry	LEAF		11	1.092	0.89	21.80		
	STEM		11	1.525	0.89	29.76		
<i>Vaccinium parvifolium</i>	TOTAL	1-6	40	3.701	0.75	39.66	75	1A1A, 1A1B, 1A1C,
red huckleberry	LEAF		40	0.632	0.78	6.30		1A1D, 1A1X, 1A2X
	STEM		40	3.065	0.68	39.27		
<i>Vaccinium sp.</i>	TOTAL	1-4	21	7.329	0.64	52.98	20	1A1G, 1A1X, 1A2E, 1A3X
	LEAF		21	1.557	0.74	9.03		
	STEM		21	5.770	0.59	46.38		
<i>Vaccinium uliginosum</i>	TOTAL	1	5	3.985	0.98	5.88	14	1D3A
bog blueberry	LEAF		5	1.230	0.97	2.03		
	STEM		5	2.756	0.96	5.07		
<i>Vaccinium vitis-idaea</i>	TOTAL	1	14	4.140	0.77	38.22	40	1A1C, 1A1X, 1A2X, 1D3A
lowbush cranberry								
<i>Viburnum edule</i>	TOTAL	1-3	9	3.102	0.95	11.68	40	1B1B
highbush cranberry	LEAF		9	1.153	0.98	2.49		
	STEM		9	1.949	0.88	11.46		
Tall Shrubs								
<i>Menziesia ferruginea</i>	TOTAL	1-6	76	5.797	0.66	65.62	50	1A1B, 1A1C, 1A1D,
rusty menziesia	LEAF		68	1.547	0.42	29.90		1A1E, 1A1X, 1A2X
	STEM		68	4.255	0.52	67.98		
<i>Oplopanax horridus</i>	TOTAL	1-5	12	2.104	0.71	11.18	15	1A1B, 1A1C, 1B1B
devils club	LEAF		12	1.617	0.76	7.40		
	STEM		12	0.487	0.41	4.77		

TABLE 2 (Cont.)

Species ¹		Layers Sampled	No. of Plots	Regression Coefficient(a)	r ²	Std Err of Estimate	% Cover Maximum	Vegetation types Sampled ²
Tall Shrubs								
<i>Rubus spectabilis</i> Salmonberry	TOTAL	1-6	43	5.912	0.82	115.36	100	1A1A, 1A1B, 1A1C,
	LEAF		43	2.552	0.89	36.49		1A1G, 1A1X, 2B1X
	STEM		43	3.360	0.55	124.44		
<i>Salix sitchensis</i> sitka willow	TOTAL	1-6	13	4.026	0.86	10.80	15	1B1B
	LEAF		13	1.348	0.94	2.34		
	STEM		13	2.618	0.86	7.25		
<i>Vaccinium alaskaense</i> Alaska blueberry	TOTAL	1-6	145	6.188	0.66	100.60	65	1A1A, 1A1B, 1A1C, 1A1D
	LEAF		145	1.041	0.63	18.39		1A1E, 1A1G, 1A1X, 1A2X
	STEM		145	5.152	0.59	99.67		
<i>Vaccinium ovalifolium</i> early blueberry	TOTAL	1-6	137	4.277	0.55	77.59	75	1A1A, 1A1B, 1A1C, 1A1D
	LEAF		137	0.927	0.78	10.01		1A1G, 1A1X, 1A2X
	STEM		137	3.354	0.44	77.94		
Tree								
<i>Tsuga heterophylla</i> western hemlock	TOTAL	1-6	53	8.869	0.83	65.36	55	1A1A, 1A1B, 1A1C, 1A1D
	LEAF		53	3.871	0.79	32.67		1A1E, 1A1X, 1A2X
	STEM		53	4.987	0.77	44.91		
<i>Tsuga mertensiana</i> mountain hemlock	TOTAL	1-6	16	17.899	0.94	46.48	25	1A1G, 1A1X, 1A2E, 1A2X

¹Nomenclature for vascular plants was based on Hulten (1974) for herbaceous plants and Viereck and Little (1972) for trees and shrubs.

²See Table 1 for explanation of codes.

TABLE 3. Biomass equations for species showing a significant difference between vegetation types. The form of the equation is $y(\text{Kg}[\ast])\text{Ha}^{-1}[\ast](10 \text{ cm vertical layer}^{-1}) = a_1[\ast] b_1[\ast] \text{coefficient1} + a_2[\ast] b_2[\ast] \text{coefficient2} + \dots + a_n[\ast] b_n[\ast] \text{coefficient}$; where $a_1, a_2, \dots a_n = 1$ or 0 depending on presence (1) or absence (0) of community type, $b_1, b_2, \dots b_n$ = percent cover of species in that community and coefficient1, coefficient2, ... coefficient are regression coefficients.

Species/Component	Coefficient	Vegetation type	Coefficient	Vegetation type	Coefficient	Vegetation type	n	r ²	Std Err of Est
<i>Athyrium sp.</i>	1.121	1A1B	2.924	1A1A 1A1C			21	.98	7.43
<i>Carex sp.</i>	2.192	1D3A	1.267	1A1G 1A1X 1A2E 1A3X			35	.85	29.91
<i>Coptis asplenifolia</i>	0.393	1A1B 1A1C 1A2E	2.590	1A1G 1A2X	0.745	1A1D 1A1X	40	.96	4.46
<i>Cornus canadensis</i>	2.348	1A1B 1A1C	6.293	1A2X	0.753	1A1D 1A1E 1A1X 1D3A	63	.75	10.18
<i>Dicranum sp.</i>	1.265	1A1X	5.476	1A1B 1A1C 1A1D 1A1G			25	.97	3.49
<i>Hylocomium splendens</i>	1.611	1A1B 1A1X	6.576	1A1A 1A1C 1A1D 1A1E 1A2X			85	.96	13.68
<i>Mnium sp.</i>	2.769	1A1B 1A1C	4.994	1A1A 1A1D 1A1G 1A2X			29	.91	2.84
<i>Tsuga heterophylla</i> TOTAL	5.746	1A1A 1A1B	10.484	1A1C 1A1D 1A1E 1A1X 1A2X			53	.89	54.26
LEAF	2.790	1A1A 1A1B	4.429	1A1C 1A1D 1A1E 1A1X 1A2X			53	.83	30.32
STEM	3.288	1A1A 1A1B	5.866	1A1C 1A1D 1A1E 1A1X 1A2X			53	.82	40.47
<i>Vaccinium ovalifolium</i> TOTAL	13.958	1A1G	3.970	1A1A 1A1B 1A1C 1A1D 1A1X 1A2X			131	.64	71.19
STEM	12.449	1A1G	3.061	1A1A 1A1B 1A1C 1A1D 1A1X 1A2X			131	.54	70.68

TABLE 4. Percent cover-biomass equations for species with both vertical layers and community differences. Equation form is the same as listed for Table 3.

Species/ Component	Coefficient	Layer	Vegetation Type	Coefficient	Layer	Vegetation Type	Coefficient	Layer	Vegetation Type	Coefficient	Layer	Vegetation Type	n	r ²	Std Err of Est.
<i>Menziesia ferruginea</i> LEAF	5.576	5	1A1X	1.191	1	1A1X	0.682	5	1A1B	0.562	1	1A1B	68	.94	9.65
					2				1A1C			1A1C			
					3				1A1D			1A1D			
					4				1A1E			1A1E			
					6				1A2X			1A2X			
<i>Rubus spectabilis</i> LEAF	0.749	1	1A1A	2.723	4	1A1A							40	.94	29.87
		2	1A1B		5	1A1B									
		3	1A1C		6	1A1C									
			1A1G			1A1G									
			1A1X			1A1X									
			2B1X			2B1X									
STEM	6.537	3	1A1A	2.235	1	1A1A							40	.73	101.94
		4	1A1B		2	1A1B									
			1A1C		5	1A1C									
			1A1G		6	1A1G									
			1A1X			1A1X									
			2B1X			2B1X									
<i>Vaccinium alaskaense</i> TOTAL	17.377	1	1A1A	8.846	2	1A1A	7.688	1	1A1B	4.084	2	1A1B	137	.82	76.19
			1A1X		3	1A1X			1A1C		3	1A1C			
			1A2X		4	1A2X			1A1D		4	1A1D			
					5				1A1E		5	1A1E			
					6				1A1G		6	1A1G			
LEAF	0.846	1	1A1A	1.689	2	1A1A	0.595	1	1A1B	0.813	2	1A1B	137	.73	15.93
			1A1X		3	1A1X			1A1C		3	1A1C			
			1A2X		4	1A2X			1A1D		4	1A1D			
					5				1A1E		5	1A1E			
					6				1A1G		6	1A1G			
STEM	16.531	1	1A1A	7.157	2	1A1A	7.092	1	1A1B	3.272	2	1A1B	137	.77	75.03
			1A1X		3	1A1X			1A1C		3	1A1C			
			1A2X		4	1A2X			1A1D		4	1A1D			
					5				1A1E		5	1A1E			
					6				1A1G		6	1A1G			

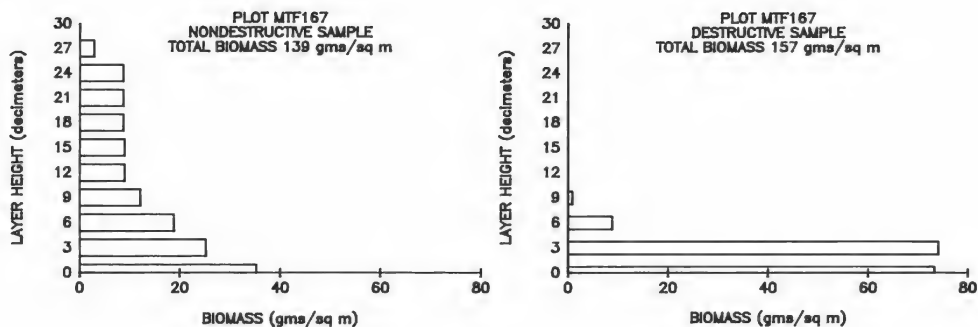


Figure 1. Comparison of biomass profiles using a destructive harvest technique and nondestructive technique for plot MTF167.

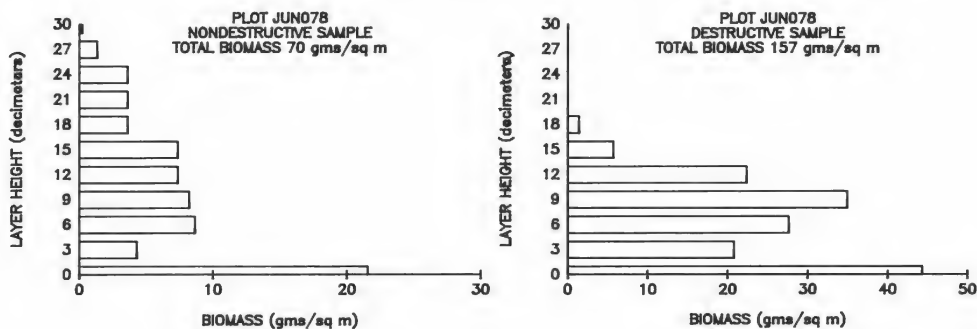


Figure 2. Comparison of biomass profiles using a destructive harvest technique and nondestructive technique for plot JUN078.

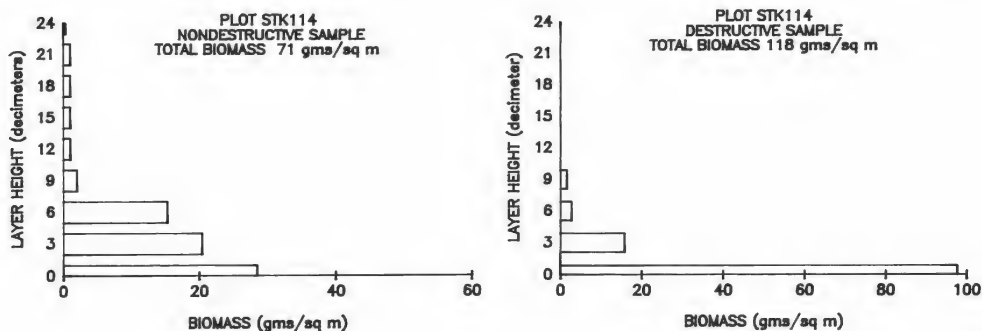


Figure 3. Comparison of biomass profiles using a destructive harvest technique and a nondestructive technique for plot STK114.

ovalifolium dropped from 77.94 to 70.68 (Tables 2 and 3).

Three of the species also showed differences in regression coefficients based on layer and vegetation type (Table 4). It was expected that lower layers may be different from upper layers especially for regressions involving stem material. This was found to be the case with both *Rubus spectabilis* and *Vaccinium alaskaense* where layer 1 was significantly different from the upper 5 layers (Table 4). A similar result was found with *Rosa acicularis* in interior Alaska (Yarie and Mead 1988). The layer 5 leaf equation for *Menziesia ferruginea* was significantly different from the lower layers (Table 4). The different layer 5 regression coefficient reflects the morphology of the shrub which often contains a tuft of leaves at the upper growing points with relatively few leaves along the length of the stem.

Horizontal-Vertical Profile

Total twig and leaf biomass of the understory estimated using the regression estimates on the H-V plots ranged from an underestimate of 11 percent (Figure 1) to an underestimate of 55 percent (Figure 2) when compared to the destructive estimate of biomass. Two of the three regression estimates fell within the 95 percent confidence limits around the average value for each plot estimated using the destructive harvest procedure. The JUN078 plot had a total twig and foliar biomass estimate using nondestructive techniques which was lower than the 95 percent confidence interval (103-210 gms/m²) around the estimate calculated using the destructive harvest technique.

A visual comparison of the vertical structure of leaf and twig biomass estimated using destructive and nondestructive techniques shows several differences. First the estimate based on nondestructive sample techniques shows greater vertical development than the estimate based on destructive samples (Figures 1-3). This difference in vertical development is very pronounced in both plots in which no understory twig and leaf biomass was found above one meter (Figures 1 and 3) based on the destructive harvest technique. This difference in estimated vertical development can be related to the differences in sampling methods. Snags with moss biomass were measured in layers higher than the ground layer

utilizing the nondestructive techniques compared to the destructive sample. This may account for the relatively low biomass values found higher in the profile of the destructive sample plots (Figures 1-3).

Second, moss biomass values in the ground layer were always greater in the destructive sample than estimated with the nondestructive technique. There is no apparent reason based on sampling differences for this result. The percent cover estimate from both sampling techniques are similar:

Plot	Sample type	
	destructive	nondestructive
	-----% Moss cover-----	
JUN078	8	15
MTF167	77	69
STK114	64	60

These results suggest a problem with the biomass equations in that they are underestimating moss biomass by 100%. If the equations presented by Alaback (1986) are used the discrepancy remains the same but instead of an underestimate we have an overestimate. For example, moss biomass was calculated as 21.6 gms/m² using the equations of this study and 93.2 gms/m² using Alaback's equation (1986). The estimate of moss biomass based on the destructive harvest technique was 44.2 gms/m².

Third, considering the different types of sampling methods and the variation in the methods used to describe each layer, both methods generally show that the same type of structure exists in the understory biomass profiles (Figures 1-3). However, there is a difference in the biomass estimates of each layer.

The largest discrepancy was found in plot MTF167 (Figure 1). The biomass predicted by the nondestructive method is primarily *Menziesia ferruginea* for the layer from 0.4 to 0.8 meters, a combination of *Menziesia ferruginea* and western hemlock (*Tsuga heterophylla*) in the layer from 0.8 to 1.5 meters, and western hemlock above 1.5 meters. The destructive sample resulted in no *Menziesia ferruginea* above 1 meter and no western hemlock above 0.3 meters. The differences in plot size (destructive sample utilized 0.56 sq meter plots while the nondestructive plot area was 100 square meters) could have resulted in the differences found between the two estimates (Alaback 1986). Also, estimates of

biomass developed from regional equations (in this case all southeast Alaska) will add to the potential error when applied to, or compared with, site specific estimates (Alaback 1987).

Based on the three comparison plots used in this study we cannot draw any definitive conclusions on which method (destructive or regression) most accurately estimates biomass structure of forests. The reliability of these estimates is very difficult to judge and there are potentially many sources of error (Alaback 1986, 1987) that can exist in both types of estimates. This study indicates that the regression approach will result

in estimates of understory biomass in vertical layers with similar accuracy as a more costly and time consuming harvest technique.

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Water Relations and Growth of Conifer Seedlings During Three Years of Cattle Grazing on a Southwest Oregon Plantation¹

Abstract

Cattle grazing, beginning one year after planting, was found to enhance water relations and growth of conifer seedlings on a young plantation in southwest Oregon. During 1984, because of the rocky nature of soils on the study area, availability of soil moisture to seedlings was assessed using the pressure chamber. Predawn xylem potentials of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Laws.) seedlings were evaluated within three levels of competing vegetation that included ungrazed, grazed, and no competition environments. For ponderosa pine, little difference in predawn xylem potentials during 1984 were detected among the three levels of competition. For Douglas-fir, seedlings on the ungrazed plots exhibited significantly more negative predawn xylem potentials earlier in the growing season in comparison to the grazed and no competition treatments. Comparison of both ponderosa pine and Douglas-fir in 1986 between grazed and ungrazed treatments revealed significantly less negative predawn potentials and significantly greater stomatal conductance on grazed plots early in the growing season. Improved water relations was one factor felt to increase growth and vigor of conifer seedlings on the grazed area. After 3 years, significantly greater seedling volume was found for both ponderosa pine and Douglas-fir on the grazed plots. Controlled cattle grazing improved plant water relations and enhanced the growth performance of young conifer seedlings.

Introduction

One important factor restricting reforestation of many forestlands in the Western United States is the failure of tree seedlings to survive on sites characterized by rapid establishment of shrub and herbaceous vegetation (Walstad *et al.* 1987). Because of accelerated juvenile growth rates exhibited by many of these competing species, resources are quickly made less available for tree growth (Radosevich and Osteryoung 1987). Previous research in the Pacific Northwest has indicated that herbaceous vegetation, particularly grasses, are competitive with young conifer seedlings (Eissenstat and Mitchell 1983, Cole and Newton 1986, McDonald 1986).

In southwest Oregon, reforestation has been particularly difficult due to the combined effects of competitive understory vegetation and dry climatic conditions (Hobbs *et al.* 1983). An important factor contributing to successful reforestation has been the control of competing vegetation for the first several years after planting (Stewart *et al.* 1984, Walstad *et al.* 1987). While silviculturists have often favored the use of

herbicides, restrictions on their use have necessitated alternative vegetation management such as manual clearing and paper-mulching to control competing vegetation.

Another vegetation management tool that may promote forest regeneration is controlled cattle grazing (Doescher *et al.* 1987). Although its potential has not been documented on mixed-conifer forests of southwest Oregon, past research has demonstrated that livestock grazing may be compatible with the objectives of forest management (Leininger 1983; Kosco and Bartolome 1983; Krueger 1986).

In 1984, we initiated a study to determine the feasibility of using cattle under operational conditions to enhance growth of ponderosa pine (*Pinus ponderosa* Laws) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings. Specifically, we hypothesized that controlled cattle grazing would improve the availability of soil moisture, and ultimately benefit the vigor and growth of conifer seedlings.

Study Area

The study area is administered by the Bureau of Land Management (BLM) in the Salt Creek

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Drainage approximately 8 km southeast of Butte Falls, Oregon (T36S., R2E, Sec. 3, Willamette Meridian). It is located at 925 meters elevation on a southwest aspect with a 35 percent slope. Vegetation of the area before harvest was characterized by species common to the hotter, drier portions of the mixed-conifer vegetation zone found in the western Cascade Physiographic and Geologic province (Franklin and Dyrness 1973). Unharvested forests adjacent to the study area were dominated by ponderosa pine, Douglas-fir, and incense-cedar (*Libocedrus decurrens* Torr.). Common understory species on the site following harvest included poison-oak (*Rhus diversiloba* T. & G.) and California fescue (*Festuca californica* Vasey).

Soils on the site have been classified as belonging to the McNabb series, which is a fine, mixed, mesic, Ultic Agriixeroll. Annual precipitation is near 762 mm (Froelich *et al.* 1982) with about 127 mm falling between May and September (McNabb *et al.* 1982). Under normal conditions, evapotranspirational demands exceed precipitation throughout this period (Johnsgard 1963). Precipitation during the 3 years of this study was considered to be less than normal.

The preharvest stand was dominated by Douglas-fir, contained approximately 162 m³/ha and had a basal area of 46 m²/ha. The site has been estimated to be a Site Class 5 for Douglas-fir (McArdle *et al.* 1961).

The harvest area was clearcut in the summer of 1982, broadcast burned that fall and planted in spring 1983 with 2.0 bare root Douglas-fir and ponderosa pine seedlings. Atrazine herbicide was applied to reduce development of competing grasses in the spring of 1983.

Methods

Experimental Design

Our study was superimposed upon a Bureau of Land Management field trial designed to investigate opportunities to seed non-native grasses into plantations for livestock and wildlife forage. A 61 m x 73 m study area was subdivided into twenty-eight 12.2 m x 12.2 m grid units. Seven grid units were sprayed with Roundup herbicide and 6 grid units with Amitrol-t herbicide in August 1983. These plus 5 other grid units were halved in October 1983 with one half receiving 20 kg/ha and the other half receiving 16.8 kg/ha

of a pasture grass mixture. The pasture species seeded onto the site included perennial ryegrass (*Lolium perenne* L., 'Linn' variety), and orchard-grass (*Dactylis glomerata* L., 'Potomac' variety). Ten of the total 28 grid units were left to revegetate naturally.

Admittedly, the BLM field trial presented a confusing array of treatments upon which to superimpose a grazing study. However, after fencing the perimeter so that cattle could be contained within the study area and cross-fencing the interior to provide one grazed and one ungrazed treatment area, the different amounts of herbaceous plants provided a unique opportunity to study grazing impacts upon conifer seedlings. The two treatment areas contained a similar array of grid units that received the previous seeding and vegetation management applications. Three levels of competition were delineated in 1984 for water relations measurements, 2 within the grazed area and 1 within the ungrazed area:

Ungrazed Treatment

Conifer seedlings selected for measurement were growing within 0.3 m of ungrazed herbaceous vegetation (UG84). We assumed that root systems of both conifers and herbaceous species would interfere with one another at this distance.

Grazed Treatment

This treatment consisted of two levels of competition under which seedlings were growing:

- 1) Seedlings growing within 0.3 m of herbaceous vegetation defoliated by cattle (G84). We made the same assumption about root system interference as in the UG84 treatment.
- 2) Conifer seedlings growing without herbaceous competition at least 1.0 m from the nearest seedling (NC84).

This range of conditions existed throughout the 1984 growing season; however, native and seeded vegetation rapidly occupied bare ground. By 1985, it was not possible to find seedlings growing without herbaceous competition. Orchard-grass, perennial ryegrass and California fescue were the dominant herbaceous species present. Although the area continued to be grazed, no data were collected in 1985.

In 1986, comparisons were made between grazed (G86) and ungrazed (UG86) conditions. Trees selected for sampling were independent of those selected in 1984. As in 1984, a similar sampling strategy was used to select trees for water relations measurements. For all measurements care was used to randomly sample within homogeneous areas and similar mixes of herbicide and seeding treatments. In addition, a

10 m x 50 m belt transect was located in the grazed and ungrazed treatment areas to measure third year conifer growth response.

Measurements

Xylem potential measurements (Waring and Cleary 1967) of Douglas-fir and ponderosa pine were made using a pressure chamber (PMS Instrument Co.). Because of the rocky soils, direct measurement of soil moisture was not possible.

In 1984, predawn xylem potentials were recorded at approximately monthly intervals beginning in June and ending in September. A sample size of three seedlings for each competitive environment was used at each sampling date. Prior to xylem potential measurement, twigs were covered with a small plastic bag to reduce transpiration, excised and wrapped in the bag and placed on ice under conditions of darkness (Turner 1981). Pressure chamber measurements were made within 30 minutes of excision.

In 1986, xylem potential measurements were initiated on May 16 and then repeated every two weeks from June 27 until September 10. A sample of six trees of each species were selected from the grazed and ungrazed areas.

In addition to xylem potential measurements, stomatal conductance of both tree species was measured using a null balance porometer (PMS Instrument Co.) on July 9, July 23, August 6 and August 20, 1986. Six permanently marked seedlings of each species, randomly selected at the beginning of the summer within the grazed and ungrazed areas, were recorded at 0800, 1100, 1400 and 1700. At the end of the day, twigs were excised, frozen, and samples brought back to a laboratory where leaf area was determined on a LI-3100 (LI-COR Inc.) area meter.

In 1986, all planted conifer seedlings in the grazed and ungrazed belt transects were measured. These measurements included: diameter at 0.02 m above the ground surface, total plant height, needle length of ponderosa pine, and number of non-nodal bud development on the Douglas-fir terminal leader. Volume of tree seedlings was computed from the formula:

$$\text{Stem Volume} = 1/3 \text{ Diameter}^2 \times \text{Height}$$

Because we only had 1 grazed and 1 ungrazed area, differences between treatments were assessed using a two sample t-test procedure (Steel

and Torrie 1980). A probability level of $p < 0.05$ was used throughout the analysis. Only significant differences are reported in this paper.

Grazing Management

Grazing was performed during 1984, 1985, and 1986 to encourage highest utilization and greatest reduction in vigor of the herbaceous vegetation. Criteria used in developing the grazing treatments were:

1. Grazing early to decrease soil moisture depletion by herbaceous vegetation and provide cattle with a high palatable forage.
2. Grazing at high intensities to remove transpiring leaf area.
3. Grazing regrowth to further reduce leaf area and suppress vigor of plants competing with tree seedlings.

Put-and-take grazing was used to control competing vegetation (Wheeler *et al.* 1973). Cattle were placed onto the plantation when the grasses were in the 4-6 leaf stage and just prior to initiation of flowering culms. Stocking rate and cattle numbers varied as dictated by the availability of forage (Table 1). Grazing was monitored on a daily basis and animals removed when reduction of forage reached a stubble height of approximately 5 cm. Careful monitoring of grazing led to minimal browsing and trampling of conifer seedlings.

TABLE 1. Cattle number and grazing use for 1984, 1985 and 1986.

Year	Grazing Period	Number of Cow/Calf Pairs
1984	May 23-May 30	1
1985	May 21-May 29	2
1985	June 6-June 9	1
1986	May 19-May 26	2
1986	June 7-June 11	2

Results

Plant Water Relations

For ponderosa pine in 1984, July 26 was the only sampling date when significant differences were detected for pre-dawn xylem potentials among treatments (Figure 1). Seedlings growing in the UG84 plots exhibited less negative xylem potentials (less stress) than those in the NC84 plots.

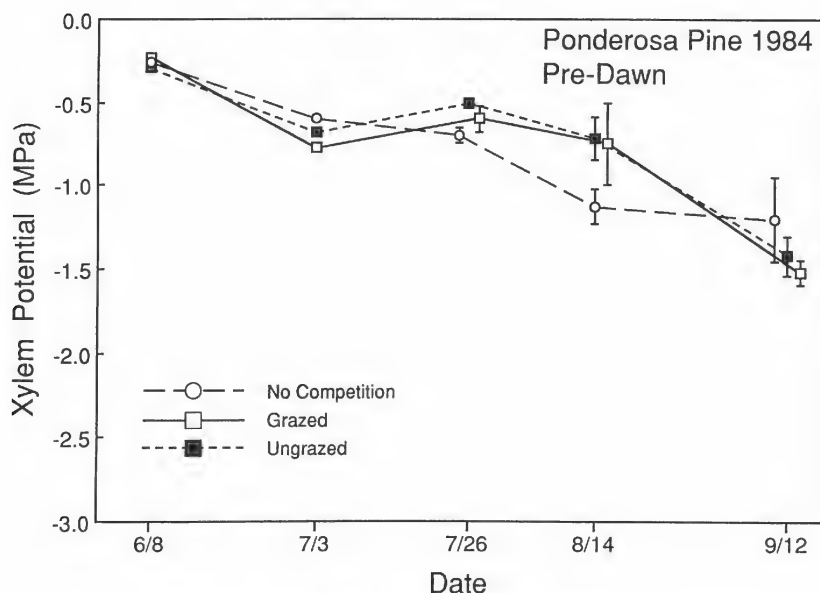


Figure 1. Predawn xylem potentials (—MPa) of ponderosa pine in 1984. Standard errors are shown about each mean unless too small to be graphically depicted.

For Douglas-fir seedlings, no differences in pre-dawn xylem potentials were detected between treatments for the June 8 and July 3 sampling dates. However, as the growing season progressed, differences between treatments became evident (Figure 2). Seedlings growing in the UG84 plots exhibited lower and more pronounced xylem potentials (more stress) on the July 26 and September 12 dates than the G84 and NC84 plots. Xylem potentials between seedlings in the NC84 and G84 plots were similar throughout the growing season except for July 26 when the NC84 plots exhibited less negative potentials (less stress). Differences in seedling xylem potential were judged not interpretable for the August 14 sampling date due to high data variation (Figure 2).

In early summer of 1986, both ponderosa pine and Douglas-fir seedlings growing in the G86 area exhibited less negative pre-dawn xylem potentials (less stress) than seedlings in the UG86 (Figures 3 and 4). However, as conifer seedlings entered into the summer months, measurement differences between the G86 and UG 86 seedlings disappeared except for two situations. On June 27, Douglas-fir seedlings on the G86 area

exhibited less negative xylem potentials (less stress) than seedlings on the UG86 area. On July 23, ponderosa pine seedlings on the UG86 area exhibited less negative xylem potentials (less stress) than those on the G86 area. No differences in pre-dawn xylem potential were detected for ponderosa pine or Douglas-fir seedlings on the other sampling dates.

While predawn xylem potential measurements apparently indicated no apparent treatment differences by mid-summer, measurement of stomatal conductance indicated ponderosa pine seedlings on the grazed area had greater physiological activity than seedlings on the ungrazed area. For example, measurement on July 9 and July 23 revealed greater stomatal conductance throughout the day for trees growing in the G86 area (Table 2). In addition, on August 6 greater stomatal conductance was found at 0800 and 1400 hours for seedlings on the G86 area. In contrast to the significant trends exhibited by ponderosa pine, stomatal conductance in Douglas-fir did not appear to differ between treatments (Table 3). Only on July 23 at 1100 hours did seedlings in the grazed treatment exhibit greater conductance than those in the ungrazed competitive environments.

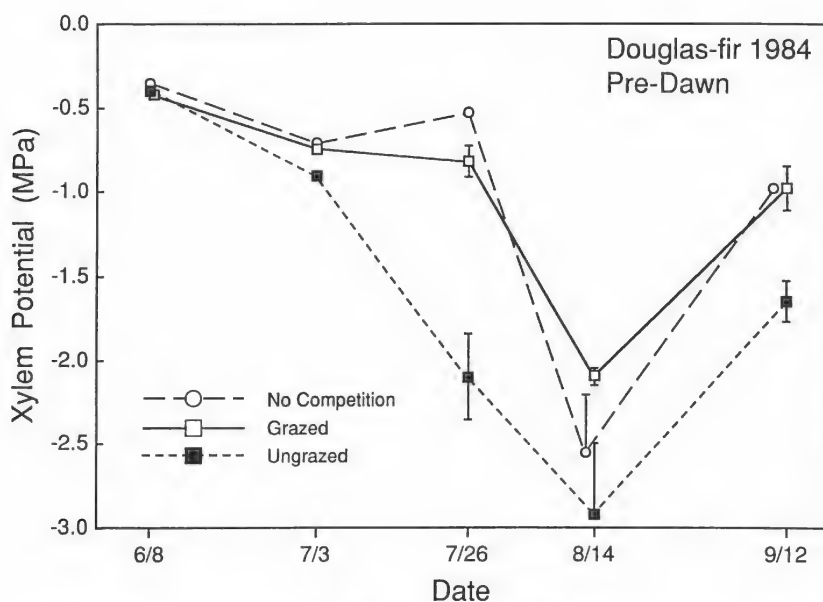


Figure 2. Predawn xylem potentials ($-MPa$) of Douglas-fir in 1984. Standard errors are shown about each mean unless too small to be graphically depicted.

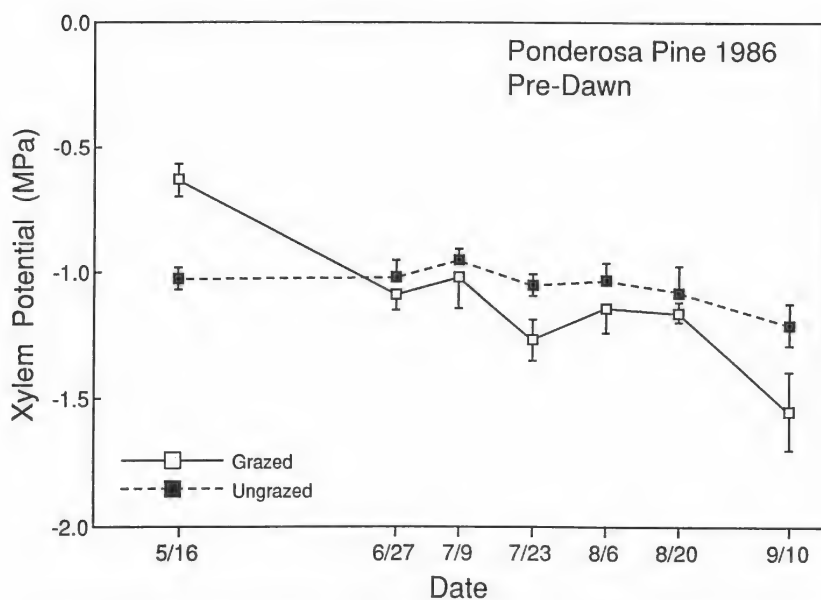


Figure 3. Predawn xylem potentials ($-MPa$) of ponderosa pine in 1986. Standard errors are shown about each mean unless too small to be graphically depicted.

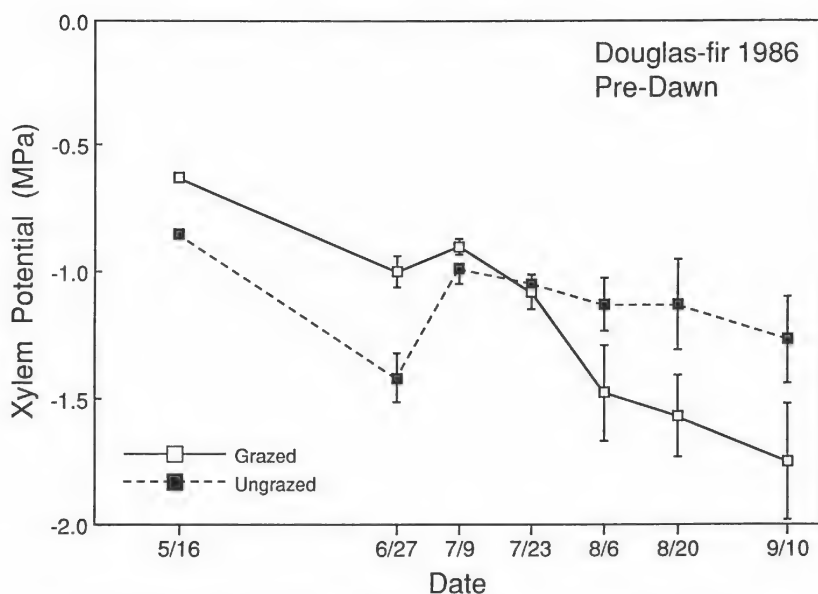


Figure 4. Predawn xylem potentials ($- \text{MPa}$) of Douglas-fir in 1986. Standard errors are shown about each mean unless too small to be graphically depicted.

TABLE 2. Stomatal conductance ($\text{cm} \cdot \text{sec}^{-1}$) of ponderosa pine in 1986 for the grazed (G86) and ungrazed (UG86) competitive environments. Standard errors are presented to the right of each mean.

Hour	Date							
	7/9		7/23		8/6		8/20	
	G86	UG86	G86	UG86	G86	UG86	G86	UG86
0800	0.45(.07)a ¹	0.33(.02)b	0.43(.07)a	0.24(.01)b	0.26(.03)a	0.18(.02)b	0.19(.01)a	0.17(0.02)a
1100	0.32(.07)a	0.19(.02)b	0.32(.06)a	0.17(.01)b	0.16(.04)a	0.10(0.01)a	0.15(.03)a	0.12(0.01)a
1400	0.21(.05)a	0.15(.02)b	0.17(.03)a	0.10(.01)b	0.11(.02)a	0.06(.01)b	0.09(.02)a	0.08(0.01)a
1700	0.17(.03)a	0.12(.02)b	0.15(.03)a	0.08(.01)b	0.08(.02)a	0.08(.01)a	0.08(.01)a	0.07(0.01)a

¹Means followed by the same letter are not significantly different ($p < 0.05$) between G86 and UG86 competitive environments at a specific date and time.

TABLE 3. Stomatal conductance ($\text{cm} \cdot \text{sec}^{-1}$) of Douglas-fir in 1986 for the grazed (G86) and ungrazed (UG86) competitive environments. Standard errors are presented in parentheses to the right of each mean.

Hour	Date							
	7/9		7/23		8/6		8/20	
	G86	UG86	G86	UG86	G86	UG86	G86	UG86
0800	0.15(.03)a ¹	0.13(.01)a	0.12(.02)a	0.09(.01)a	0.10(.02)a	0.10(0.01)a	.08(.03)a	.09(.01)a
1100	0.08(.02)a	0.06(.01)a	0.07(.01)a	0.03(.004)b	0.05(.02)a	0.04(0.01)a	.06(.03)a	.04(.01)a
1400	0.06(.01)a	0.06(.01)a	0.05(.01)a	0.03(.004)a	0.03(.01)a	0.03(0.01)a	.03(.02)a	.04(.01)a
1700	0.05(.01)a	0.05(.01)a	0.03(.01)a	0.06(.01)a	0.03(.01)a	0.03(0.004)a	.03(.01)a	.03(.01)a

¹Means followed by the same letter are not significantly different ($p < 0.05$) between G86 and UG86 competitive environments at a specific date and time.

Growth Measurements

After 3 years of grazing, growth and vigor of the 4-year-old Douglas-fir and ponderosa pine were enhanced on the grazed treatment (Table 4). The following seedlings characteristics were greater in the grazed area:

- (1) Larger diameter at 0.02 m aboveground for both ponderosa pine and Douglas-fir.
- (2) Greater total height for ponderosa pine, but not Douglas-fir.
- (3) Greater volume of both ponderosa pine and Douglas-fir.
- (4) More lateral buds on Douglas-fir terminal leaders.
- (5) Greater needle length on ponderosa pine terminal leaders.

Discussion and Conclusions

Results of this research lend support to the hypothesis that appropriately timed grazing can improve the availability of soil moisture and ultimately benefit the vigor and growth of tree seedlings. A key finding of this case study was increased conifer growth and vigor in the grazed treatment. Leininger (1984) also found improved growth of Douglas-fir seedlings in the Oregon Coast Range on plantations grazed by sheep. This was in a generally wetter environment, with shrubs instead of grasses being the primary competing species. Other researchers however, have been unable to demonstrate enhancement in conifer growth on areas grazed by livestock. For example, McDonald and Fiddler (1988) studied the use of sheep to release ponderosa pine from deerbrush (*Ceanothus integririmus* H. & A.) in the northern California Sierras. They found signifi-

cant reductions in brush cover and height, but no differences in conifer growth between grazed, hand-grubbed and control treatments. McDonald and Fiddler believed that the degree of browsing by sheep was not enough to significantly reduce shrub vigor, particularly competition resulting from root interactions.

We believe that several mechanisms may have enhanced seedling performance. First, intensive grazing of competing vegetation may have reduced transpirational surface area and increased soil moisture availability to tree seedlings. This contention is supported by several researchers who have found that heavy defoliation of pasture grasses by cattle increased soil moisture, particularly during the early portions of the growing season (Svejcar and Christensen 1987, Wraith *et al.* 1987). Second, intensive defoliation may have reduced root development of competing vegetation (Crider 1955, Richards 1984). Smaller root systems of grazed plants could ultimately result in a greater soil volume available for exploitation by root systems of conifer seedlings. Third, grazing may have also enhanced availability of light to young tree seedlings. In forested ecosystems where adequate soil moisture is present for seedling growth, grazing during the early years of plantation establishment could help reduce competition for light from aggressive seral vegetation. Fourth, there is speculation that livestock, through the deposition of dung and urine, may help enrich soil nutrients such as nitrogen (Leininger 1984). Finally, cattle through hoof action may have modified soil surface characteristics, such as surface roughness, and allowed for greater infiltration of precipitation. Although each of these factors may have resulted in improved growth and/or water

TABLE 4. Mean growth measurements of ponderosa pine and Douglas-fir in 1986 for the grazed (G86) and ungrazed (UG86) competitive environments. Standard errors are presented to the right of each mean.

Competitive Environment	Ponderosa Pine		Douglas Fir	
	G86	UG86	G86	UG86
Diameter (cm)	3.3(0.11)a	2.6(0.11)b	2.1(0.10)a	1.6(0.06)b
Height (cm)	94.4(3.3)a	82.1(3.2)b	74.6(3.5)a	69.5(3.1)a
Volume (cm ³)	388.0(36.0)a	213.5(26.3)b	137.5(16.0)a	71.02(9.0)b
Non-Nodal Buds (Nos.)	—	—	6.1(.44)a	4.5(0.52)b
Needle Length (cm)	16.7(0.33)a	14.5(0.44)b	—	—

¹Similar letters denote nonsignificant differences ($p < 0.05$) between seedlings in the G86 and UG86 competitive environments.

relations of conifer seedlings, a more controlled experimental approach is needed to elucidate specific causal factors. These factors could provide the basis for future research.

An interesting result of this research was the 1986 contrast between stomatal conductance and xylem potential for ponderosa pine. Conductance was high in the grazed area during July and August 1986 in comparison to trees on the ungrazed area. However, xylem potential readings during this same period either did not differ between the two competitive environments (July 9, August 6), or were more negative (more stress) on the G86 area (July 23). Despite these mixed results, our growth and vigor findings suggest that seedlings on the grazed area had greater health and vigor than seedlings on the ungrazed area.

One explanation for the contrasting patterns may be that xylem potentials on the UG86 area were reduced because of shading from the tall, mature grass. It is important to note that xylem potential values for ponderosa pine seedlings in both competitive environments remained within the range reported for active growth. The predawn values in the grazed area did not drop below -1.3 MPa until September, while values for the ungrazed environment did not drop below -1.3 MPa for the season. This is less than the -1.8 MPa reported by Running (1976) for stomatal closure. While conductance measurements are not available from May to June to show transition into July, the higher conductances shown by ponderosa pine later in the summer support the idea of greater physiological activity of seedlings in G86 plots. Also, other studies of *Pinus* spp. document that needle length is sensitive to nutrient and water stress, with responses in one year likely indicators of future vigor (Gar-

rett and Zahner 1973, Timmer and Morrow 1984). Volume measurement of ponderosa pine further confirms the greater vigor of seedlings on the G86 area.

While trends in water relations are less clear for Douglas-fir, individuals in the G86 area have substantially larger volume than those in the ungrazed area. This reflects a better environment for growth during the 3 years of grazing. Tappeiner *et al.* (1987) have demonstrated that increased lateral bud production is also highly correlated with future tree growth. Therefore, the increased numbers of buds in the G86 plots probably suggest the potential for greater vigor and growth of these seedlings in the near future.

In conclusion, this case study suggests that application of appropriately timed cattle grazing, like application of herbicides, may provide ecological benefits to planted conifer seedlings in southwest Oregon. Enhanced water availability promoted by cattle grazing appears to be one factor leading to larger ponderosa pine and Douglas-fir seedlings. Other factors not measured in this research, such as changes in nutrients, light and soil properties, may have also contributed to improved growth of conifer seedlings.

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Shallow Tillage Fails to Increase 5-Year Growth of Ponderosa Pine Seedlings

Abstract

Forest soils can be compacted by rubber-tired skidders and crawler tractors during timber harvesting and site preparation. Compacted soils are often tilled with machines pulling rock rippers to reduce detrimental effects on seedling performance. In southwest Oregon, soil compaction during intensive site preparation by machines increased the naturally high bulk density of the soil by 9 percent at the 10- to 20-cm depth. Subsequent tillage with machine-mounted rock rippers, spaced 1.68 m apart, to a depth of 30 cm significantly reduced the bulk density of approximately six percent of the soil to that depth. Through year five, tillage did not increase growth of 2-0 bareroot seedlings of ponderosa pine (*Pinus ponderosa* Laws.) planted in the rip-furrow compared to those planted midway between furrows. Survival was at least 96 percent for both planting locations. These results suggest that shallow tillage of soil is ineffective at improving the performance of well-planted seedlings.

Introduction

Soil compaction by tracked or wheeled machines during timber harvest and site preparation commonly reduces the productivity of forest sites (Froehlich 1979, Greacen and Sands 1980). This problem is particularly serious in the Pacific Northwest, where soils often have low bulk densities and are easily compacted (Froehlich and McNabb 1984). Unfortunately, some undisturbed, drier forest sites in southwest Oregon have bulk densities higher than those of compacted soils reported to cause long-term loss of site productivity (Wert and Thomas 1981). And even soils with naturally high bulk densities may be compacted (Howard *et al.* 1981).

Tillage with rock rippers is a common site preparation after machine harvesting and slash piling. Although the benefits of tillage on seedling survival and growth have not been investigated on Northwest soils with high bulk density, much world-wide evidence suggests that such a practice can significantly increase survival, growth, or both (Andrus and Froehlich 1983). In Australia and New Zealand, tillage with rock rippers is reported to increase seedling survival by as much as 38% and growth by even more (Ritchie 1965, Guild 1971, Berg 1975, Craig *et al.* 1977). The practice appears to be most successful on sites with shallow, stony soils or in areas of low precipitation (Ritchie 1965, Guild 1971), descriptions that typify many sites in southwest Oregon.

In 1981, we began a study to evaluate how soil ripping affects the field performance of

ponderosa pine (*Pinus ponderosa* Laws.) seedlings planted on a hot, dry site in southwest Oregon. The site was prepared and ripped prior to installation of the study. Seedlings were planted in the center of the rip-furrows and halfway between furrows as a means of comparing seedling performance in tilled and nontilled soil, respectively. Rip-furrows were evenly spaced across the site, so we measured bulk density along several short transects oriented at right-angles to the furrow to determine the actual volume of soil loosened by the rock rippers. Bulk density was also measured in an adjacent undisturbed area; comparison of these data with the bulk density of nontilled soil provides a measure of soil compaction during site preparation.

Past research has found that the growth of ponderosa pine is significantly reduced when the bulk density of compacted soil is less than the natural bulk density on our site (Cochran and Brock 1985, Helms and Hipkin 1986, and Helms *et al.* 1986). In our study, soil ripping did not enhance field performance. We offer our negative results as an inducement for re-evaluating such practices and encouraging further research.

Site Description and Methods

The study site was in southwest Oregon approximately 20 km southwest of Medford (123° 3' W. Lat., 42° 15' N. Long.) on a 30 percent, south-facing slope. The soil is a moderately deep, fine-loamy, mixed, mesic Typic Haploxeralf of the Vannoy series. The area receives approximately 700 mm of precipitation annually (Froehlich *et al.*

1982), with less than 190 mm occurring between May 1 and September 30 (McNabb *et al.* 1982). Prior to this study, the site was occupied by a brushfield that developed after wildfire in the late 1930s. The brushfield was dominated by white-leaf manzanita (*Arctostaphylos viscida* Parry), 3 to 4 m tall, and contained scattered Oregon white oak (*Quercus garryana* Dougl.), Pacific madrone (*Arbutus menziesii* Pursh), buckbrush (*Ceanothus cuneatus* (Hook.) Nutt.), poison oak (*Rhus diversiloba* T. & G.), and annual grasses and forbs.

Site preparation started in early July 1980 after nearly a month of dry weather. The work was performed in three distinct operations—brush uprooting, brush piling and burning, and soil ripping. Brush was uprooted with a D-6 Caterpillar® tractor with a slash rake attached to the dirt blade. A 955k Caterpillar® tractor with a Young loader grapple-rake then piled the brush, which was burned in the fall. The 955k was equipped with a tool bar and two 46-cm rock rippers spaced 1.68 m apart; it was used to rip the area in accordance with ground contour.

In spring 1981, 160 bareroot 2-0 ponderosa pine seedlings were planted with shovels. Eighty seedlings were planted in the center of the rip furrows while the remaining 80 were planted in rows mid-way between furrows in unripped soil. No seedlings were planted in or near burn piles. Seedling heights and diameters at 2.5 cm were measured immediately after planting and annually during the fall for the next 5 years. After five years, eight seedlings in each treatment were excavated and the roots examined for morphological changes from the treatments.

One year after the site was prepared, soil bulk density was measured along eight randomly selected transects established at a right angle to the rip-furrow. Transects were 1.68 m in length and centered across the rip-furrow; the length approximately equals the spacing of rip-furrows. Bulk densities were measured in the center of the furrow and 10, 23, 32, and 84 cm on either side of it; measurements were more closely spaced near the center of the rip-furrow to more accurately estimate the 'V-shaped' volume of soil loosened by the rippers. The greatest distance was halfway between furrows, and is representative of the nonripped soil condition. At each point on the transect, bulk density was measured at depths of 5, 10, 15, 20, 25, and 30 cm. Thus, bulk density was measured at 72 locations, and when combined

with the six measurements at each location, result in a total of 432 bulk density measurements in the planted area. As an estimate of pretreatment values, bulk density was also measured at eight locations and six depths in the adjacent undisturbed brushfield about 50 m upslope from the planting site; the soil was of the same series but, on the average, contained fewer coarse fragments below about the 25 cm depth.

Wet bulk density was measured with a double probe gamma gauge using previously developed calibration curves (Froehlich *et al.* 1980). Access holes for the probes were installed parallel to the rip-furrow. After bulk density was measured at each point on the transect, two soil samples, one each from the 0- to 15-cm and 15- to 30-cm depths, were removed from between access holes and analyzed from gravimetric moisture content; spatial and vertical variation of soil moisture was small. Soil moisture contents used to convert bulk densities from a wet to a dry weight basis were less than 15 percent and varied less than 3 percent at each location.

Bulk densities in the center of the rip-furrow, midway between furrows (84 cm location), and in the undisturbed brushfield were analyzed for significant differences by Duncan's new multiple-range test (Steele and Torrie 1980). Differences in mean size of seedlings on ripped and unripped positions were tested by a one-way analysis of variance. Prior to analysis, percentages of survival were subject to the arcsine transformation (Steele and Torrie 1980).

Results

Bulk density

Although the 1.68 m spacing of rip-furrow across the site gave the appearance of a successful tillage operation, the wide spacing of the furrows reduced the potential effectiveness of the tillage operation (Andrus and Froehlich 1983). Bulk densities in the middle of the rip-furrows as far down as 20 cm were significantly less than those midway between furrows (Table 1). Below 20 cm, bulk densities of soil in these two areas were not significantly different. This significant reduction in bulk density was limited to the surface soil because the rock rippers did not penetrate more than about 30 cm, as evidenced by a cross-sectional profile of bulk density (Figure 1). The profile confirms visual observations that less than 25 percent

TABLE 1. Mean bulk densities (Mg/cm^3) at various depths in site-prepared and tilled soils in the middle of and midway between rip-furrows and in an adjacent, non-site prepared brushfield.¹

Sampling Location	Soil Depth (cm)					
	5	10	15	20	25	30
Midway between furrows (unripped)	1.25b	1.47c	1.49b	1.47b	1.51b	1.56b
In middle of furrows (ripped)	1.06a	1.19a	1.28a	1.35a	1.49b	1.58b
Adjacent brushfield (nonprepared)	1.27b	1.35b	1.37a	1.35a	1.34a	1.40a

¹Within a column, means followed by the same letter are not significantly different at $p = 0.05$.

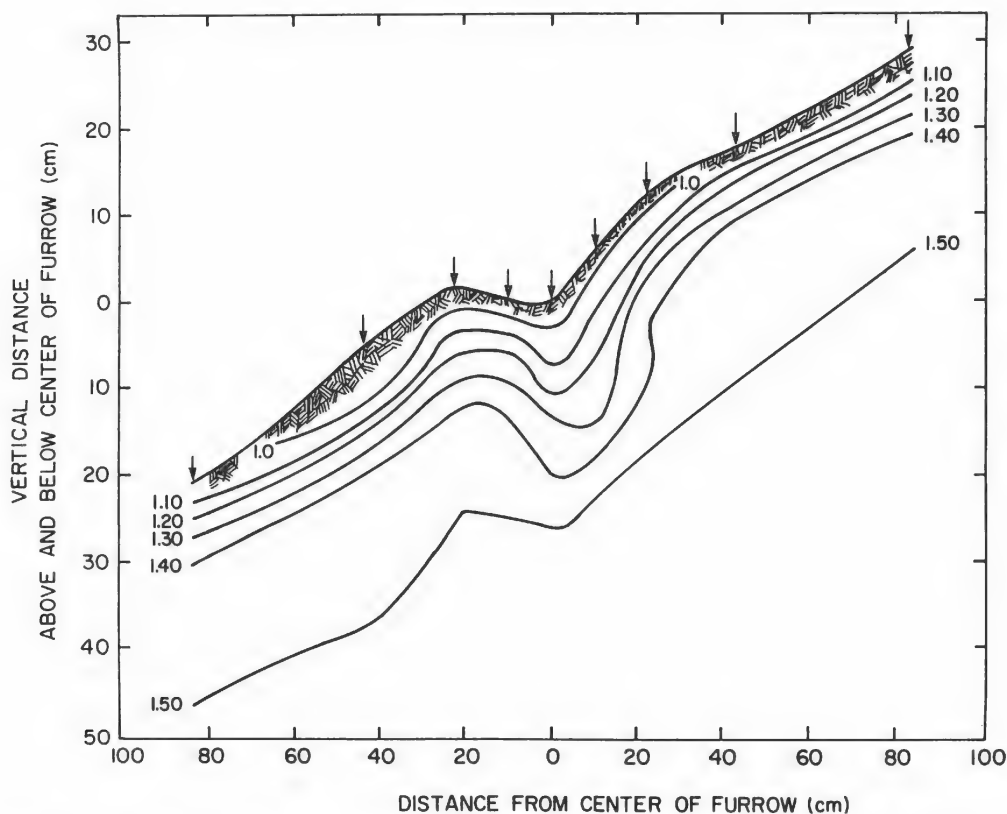


Figure 1. Cross-sectional profile with isolines of dry bulk density following tillage with a single-tine rock ripper. Average of eight transects across different rip-furrows, all of which traverse the site. Arrows identify location of gamma gauge for measuring bulk density at 5 cm depth increments.

of the soil surface showed evidence of tillage and a significant reduction in bulk density was limited to approximately six percent of the surface 30 cm of soil. The small volume of tilled soil is attributed to the shallowness of tillage, the wide spacing of the rock rippers, and the single pass of the machine (Andrus and Froehlich 1983).

The content of rock fragments below 20 cm increased substantially at several locations in the ripped area but was generally absent in the brushfield. This disparity made comparisons of these bulk densities uncertain because rock fragments increase the bulk density of soil measured with a densimeter. Few rock fragments were found at any location above 20 cm; thus, comparisons among treatments at these depths were possible.

Bulk densities of rip-furrows were significantly less than those of the nonprepared brushfield to a depth of 10 cm (Table 1). Although bulk densities at 5 cm were similar midway between the rip-furrows and in the brushfield, those between 10 and 20 cm were significantly higher in the site-prepared area. This increase averaged 9 percent and probably resulted from soil compaction during the intensive use of machines for site preparation. The surface 5 cm of soil midway between the rip-furrows may have been loosened by natural processes in the 12-month period bounded by site preparation and measurement of bulk densities.

Seedling Performance

First-year survival was excellent—98 percent for seedlings planted in rip-furrows and 99 percent for those planted midway between furrows. This high survival occurred despite unusually dry and hot weather during spring and summer. Only one storm as intense as 2 cm of rain in 2 days occurred from the time the seedlings were planted until early October. During August, daily air temperatures above 40°C set several record highs for the region.

During the second year, survival decreased to 96 percent for seedlings planted in rip-furrows but remained unchanged for those planted midway between furrows. No further mortality of seedlings was measured in succeeding years.

Excavation of eight root systems from each treatment did not indicate a preferred orientation of roots along the furrow; only one seedling had a root following the furrow for more than a few centimeters and all seedlings had one or more large roots penetrating the bottom of the furrow. The largest trees had roots nearly 1 cm in diameter to a depth of 1 m; hence, the shallow ripping would have little effect on the growth of these roots.

Although seedlings planted midway between furrows were consistently larger than those planted in the furrows, differences in annual growth and total seedling size were never statistically significant. After 5-years, the total diameter and height of seedlings planted in rip-furrows were 4.39 cm (S.E. $\pm$ 0.15) and 117 cm (S.E. $\pm$ 4.8), respectively, while the total diameter and height of seedlings planted between furrows were 4.54 cm (S.E. $\pm$ 0.16) and 121 cm (S.E. $\pm$ 4.2), respectively.

Discussion

The 1.68 m between ripper shanks on the machine used in this study was wider than typical of most operations where large machines pull at least three rippers. The wide spacing of rippers coupled with their shallow penetration of the soil (Figure 1), resulted in the bulk density of surface 20 cm of soil being significantly reduced over about 10 percent of the area. Considering that roots of 5-year-old seedlings extend below 1 m, shallow tillage loosened less than 2 percent of the soil potentially occupied by roots. This suggests that seedlings planted in rip-furrows failed to increase in size because of insufficient soil tillage. Although speculative, this seems a reasonable hypothesis based on the results of other studies (Andrus and Froehlich 1983). High seedling survival, regardless of treatment and climatic extremes, probably reflects the overall emphasis placed on the careful planting of high quality seedlings and control of competing vegetation (Cleary *et al.* 1978).

Tillage studies have shown that seedling response is greatest when soils are tilled to depths greater than 50 cm (Ritchie 1965, Guild 1971, Berry 1979). Under optimum moisture conditions, deep tillage not only increases the depth to which soil is loosened but also the areal extent (Andrus and Froehlich 1983). These factors

help explain the greater response of seedlings to deep tillage and suggest why shallow tillage of this site failed to improve seedling performance. Furthermore, rock rippers are poorly suited implements for tilling soil because of their design (Andrus and Froehlich 1983). Implements specifically designed for tilling soil, such as winged rippers, lift and fracture much larger volumes of soil, particularly at greater soil depths. Thus, the failure of ripping to improved seedling performance on this well-prepared site suggests that the efficacy of tillage operations must increase if the practice is to result in improved seedling performance and that additional studies are needed to determine the benefits of such tillage.

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Introductory Notes on Squarrose Knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugl.)

Abstract

Squarrose knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugl.), previously unrecorded in Oregon, was discovered in August 1988 near Long Creek in Grant County. It has spread from initial infestations in California and Utah (1950 and 1954, respectively) to occupy an estimated 5,000 ha of rangeland and pasture in three states.

Two exotic seed head gall forming insects, *Urophora quadrifasciata* and *U. affinis*, were found using the Oregon squarrose knapweed population. *Urophora quadrifasciata* galls were found in 79 percent of the seed heads. Because only 36 percent of the knapweed heads contained filled seeds and the deciduous heads are disseminated epizooically, the flies may slow spread of the weed.

Squarrose knapweed is a relatively new and unknown weed that has the potential to reduce forage production similar to losses due to other knapweeds on rangeland in the western United States. New line drawings illustrate important characteristics of the plant as an aid to identification.

Introduction

Since the turn of the century, several knapweeds and starthistles (*Asteraceae: Centaurea* spp.) have become serious rangeland and pasture weeds in the western United States. Introduced *Centaurea* species have gained the reputation of being aggressive and weedy. This investigation of squarrose knapweed, *C. virgata* Lam. ssp. *squarrosa* Gugl., was motivated by the discovery of a population in eastern Oregon by Dan Sharratt, Agronomist, Oregon Department of Agriculture, in August 1988. Previously known in the western U.S. only from California and Utah, squarrose knapweed is native to Bulgaria, Lebanon, Anti-Lebanon, Transcaucasia, northern Iraq, Iran, Afghanistan and Turkestan (Wagenitz 1975).

The purpose of this study was to document the distribution of squarrose knapweed in California, Oregon, and Utah, and to report the use of squarrose knapweed as a host plant by *Urophora quadrifasciata* (Meigen) and *U. affinis* (Fraeunfeld) (Diptera: Tephritidae), insects introduced for the biological control of diffuse and spotted knapweed, *C. diffusa* Lam. and *C. maculosa* Lam., respectively, in North America (Harris 1980a, Maddox 1982).

Description of the plant (Figure 1)

The following description of squarrose knapweed is based on Bellue (1952), Abrams and Ferris (1960), Tingey (1960), Munz and Keck (1973),

Wagenitz (1975), Holmgren and Andersen (1976), and Welsh *et al.* (1987).

Squarrose knapweed is a taprooted perennial with a woody base and several stems 0.3 to 0.9 m tall, profusely branched with rigid spreading branches. The crown consists of one or more clusters of rosette leaves branching from a stout taproot. Deeply dissected basal leaves often wither by flowering time. Stem leaves have fewer segments, upper ones are bract-like. Numerous flower heads are borne singly or in pairs at the ends of branches. Flowers are rose-purple or pink. The flowering period is June to August. Heads are slender urn-shaped, 7 to 9 mm long and 3 to 4 mm wide. The terminal spine of the involucre bracts is conspicuously stouter and longer than the 4 to 6 pairs of lateral spines and is usually spreading or recurved. Bracts are pale or suffused with red or purple, especially near the tip. Each head comprises 4 to 8 (occasionally 10) hermaphrodite flowers. Capitula (seed heads) are closed and deciduous at fruiting time. Achenes (cypsels) are 3 to 3.8 mm long with a pappus 0.5 to 3.5 mm or absent.

History in California and Utah

Squarrose knapweed was collected from Big Valley, Lassen County, California, in July and August 1950 (Howell 1959). In 1950 the squarrose knapweed on the Kramer Ranch in Big Valley extended about 90 m from both sides of the road into a recently disked summer fallow

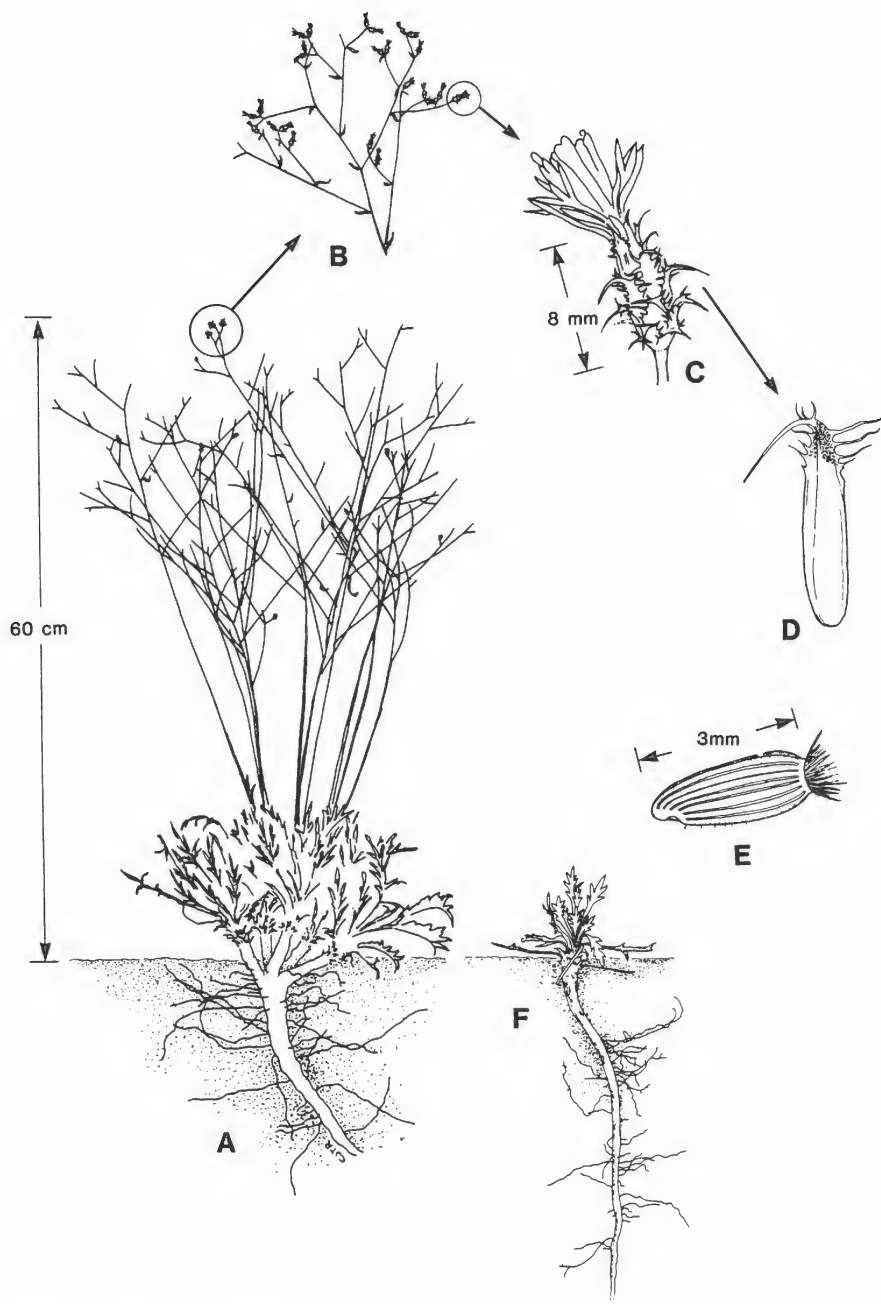


Figure 1. Squarrose knapweed: A) mature plant with old flower stems; B) branching pattern of flower stem; C) flower head; D) bract; E) seed; F) taprooted rosette prior to flowering. Mature plant and rosette were drawn from Utah specimens, the others from Oregon specimens. Collections by the authors are filed in the Marion Ownbey Herbarium, Washington State University, Pullman.

field on one side and a stand of grain on the other (Bellue 1952). A history of the Lassen County population written by J. B. Phillips (Bellue 1952) indicates that squarrose knapweed was first noted about 1934-1937, by the lessee who used the ranch as sheep pasture. The land was also used as an overnight campground by several sheep men when they trailed their bands from the Sacramento Valley to higher ranges in the summer and returned them in the fall.

In Utah, the weed was first collected from Tintic Junction, Juab County, in August 1954 (Howell 1959). Minutes of a meeting concerning squarrose knapweed held in Nephi, Utah, in November 1954, indicate that the weed was seen near the grain elevators in 1928, and that a seed company employee in Delta observed its occurrence in 1938 (B. Jones, pers. comm.). In 1954 the weed was found in varying densities over an area of about 1300 ha of depleted rangeland west of Tintic in Juab County (Tingey 1960).

Methods

Distribution Survey

Known populations in California, Oregon, and Utah were assessed by contacting individuals in each area. Survey data were provided for California by the Weed Project Leader for the Department of Food and Agriculture and the Siskiyou County Agricultural Commissioner. Accurate records of squarrose knapweed locations were available in California because the potential for spread and the opportunity for containing or eliminating localized infestations was recognized as early as 1974 when it was recommended that the squarrose knapweed rating be changed from control at county discretion (Class B weed) to eradication at the State level (Class A weed) (L. Sonder, pers. comm.). The eastern Oregon Agronomist for the Department of Agriculture recorded the extent of the Oregon infestation after walking the area, noting boundaries and looking for outlier plants. In Utah the State Extension Weed Specialist, Juab County Extension Agent and Weed Supervisor, and Range Conservationist for the Bureau of Land Management (BLM) Fillmore office provided distributional information. The estimates in Utah are less precise but were done by those individuals who have worked in the squarrose knapweed control program and have observed the infestations.

Urophora Species in the Oregon Population

Mature seed heads were collected from squarrose knapweed plants at Long Creek, Oregon, on 24 August 1988. Five hundred heads were dissected to determine the level of parasitism and the effect on seed production. The number of insect galls and the number of filled seeds (achenes) per head were recorded. No differentiation was made between first and second generation *Urophora quadrifasciata* galls; some heads contained both. Weight of filled seeds and size of seed heads (length and width of dry capitula) were also recorded. Filled seeds were a shiny golden brown and shaped like the illustration in Figure 1E. Unfilled seeds were pale, flat and lightweight.

Results

Squarrose Knapweed Distribution (Figure 2)

Four counties in California report infestations: Lassen, 500 ha scattered over 1,200 ha; Modoc, 2 ha scattered over 30 ha; Shasta, 20 ha scattered over 50 ha (L. Sonder, pers. comm.) and Siskiyou, 120 ha (E. Hale, pers. comm.). The main area of recent expansion in California has been in Shasta County. Squarrose knapweed occurs primarily on pasture and rangeland, except for Modoc County, where it is still on roadsides (L. Sonder, pers. comm.). In Oregon, squarrose knapweed infests approximately 250 ha of rangeland 3 km west of Long Creek, Grant County (D. Sharratt, pers. comm.). The native vegetation is a juniper/fescue, *Juniperus occidentalis*/*Festuca idahoensis* association (Franklin and Dyrness 1973). The core of the Utah population is estimated at 4,000 ha, with 5 counties affected: Juab, Tooele, Millard, Utah, and Sanpete (S. Dewey, pers. comm.). Scattered plants have been found over a 15,000 ha area of BLM land west of Tintic Junction (H. Gates, pers. comm.). No estimate of the amount of area actually infested with squarrose knapweed within these boundaries is available.

Urophora flies and seed production (Long Creek, Oregon population)

One *Urophora affinis* gall was found, indicating that this insect can utilize squarrose knapweed as a host plant. *Urophora quadrifasciata* galls were found in 79% of the squarrose knapweed heads (Table 1). This fly lays eggs in the developing knapweed buds and each larva replaces a

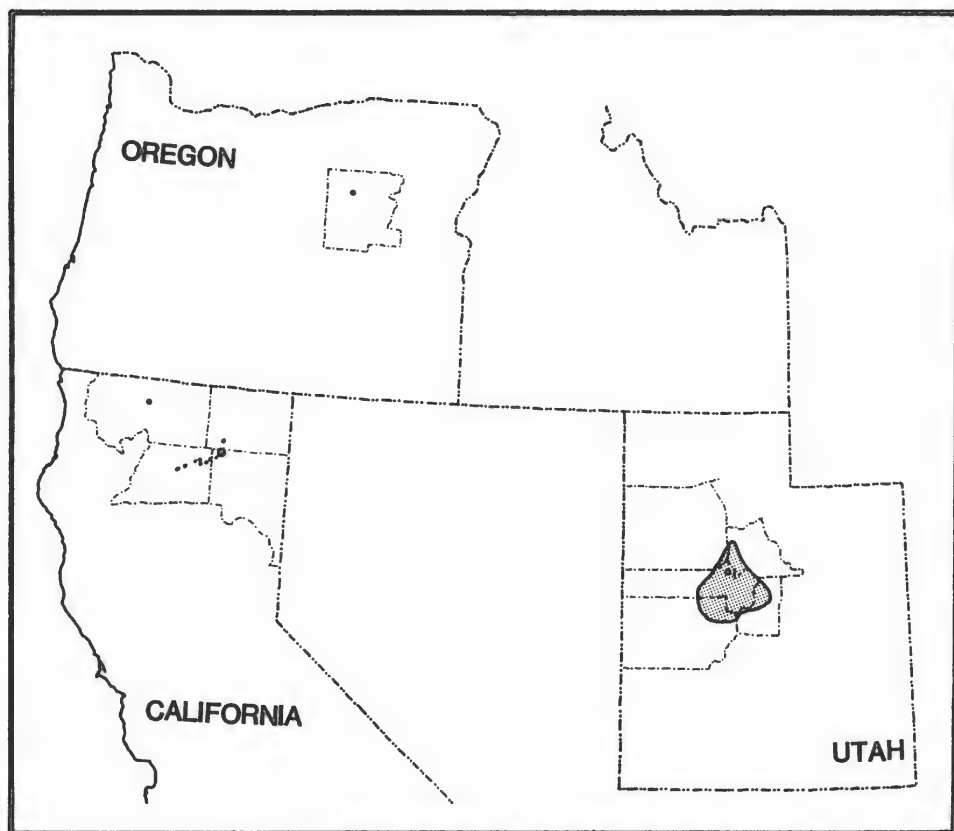


Figure 2. Location of squarrose knapweed populations in California, Oregon, and Utah. No detailed survey has been done in Utah. All known infestations occur within the shaded area.

TABLE 1. Effect of *U. quadrfasciata* gall load on squarrose knapweed seed production

Galls/ Seed Head	% of Seed Heads ¹	Filled Seeds/ Seed Head Mean $\pm$ Standard Deviation
0	21	1.79 $\pm$.85
1	24	.58 $\pm$.78
2	24	.14 $\pm$.47
3	18	.11 $\pm$.35
4	9	.02 $\pm$.15
5	3	.06 $\pm$.25
6-8	1	-0-

¹Sample size = 500

seed. The seed coat and pappus were often visible surrounding the insect puparium. The maximum number of galls found per head was 8, corresponding to the total number of flower ovaries normally available. Seed production was dramatically reduced with a single gall per head (Table 1). Seeds per head correlated negatively ($r = 0.86$) with increasing gall number through 4 galls. Sixty-four percent of the heads produced no filled seeds (Table 2). Heads without filled seeds contained one or more galls (Table 2). All of the sampled ungalled heads contained at least one seed. Total seed production from the 500 heads was 289 seeds. The average number of seeds per gram was 360 seeds. The sampled squarrose knapweed heads averaged 8.8 mm long and

TABLE 2. Mean number of galls associated with different levels of seed production

Filled Seeds/ Head	% of Seed Heads ¹	Galls/Seed Head Mean $\pm$ Standard Deviation
0	64.0	2.51 $\pm$ 1.2
1	20.0	.88 $\pm$ 1.2
2	11.0	.38 $\pm$ 0.7
3	4.4	.23 $\pm$ 0.5
4	.4 (2 heads)	-0-
5	.2 (1 head)	-0-

¹Sample size = 500

and 4.2 mm wide (including spines). Unsampled smaller heads may have contained neither galls nor seeds.

Discussion

In the Flora of Turkey, the U.S. specimens key to subspecies *squarrosa* (Group A) of *Centaurea virgata* which is found mainly in Inner Anatolia (Wagenitz 1975). Squarrose knapweed has been listed as a biennial in at least one source (Keffer 1978), but other floras (Abrams and Ferris 1960, Wagenitz 1975) and our field observations in Oregon and Utah indicate that it is a perennial. Small rosettes have large taproots and successive rows of weathered leaf bases indicating that they are not seedlings and several years of growth may be required before flowering. Crowns that branch from under the soil surface to form multiple rosettes and an accumulation of bare, weathered flower stalks are characteristic. The morphology that indicates perennial growth form also appears to be an adaptation to harsh growing conditions, such as cold temperatures and drought.

The seed dissemination habit of squarrose knapweed is unique among adventive *Centaurea* species in the western U.S. Other *Centaurea* species are spread as individual seeds carried by vehicles, irrigation water, crop seed contaminants, or as entire plants moved by wind or vehicles. Historically, most movement of squarrose knapweed in the western U.S. has been associated with sheep (Bellue 1952, Tingey 1960, H. Gates and L. Sonder, pers. comm.) It is ideally suited to this mode of transport because the recurved spines of the capitula, like those of burdock (*Arc-tium*) or cocklebur (*Xanthium*), perfectly comple-

ment the wool of sheep in a manner analogous to a Velcro® fastener. At fruiting time, the heads are closed (retaining the seeds) and deciduous; consequently seeds are readily spread by animal wool, hair or fur (Wagenitz 1972). No reference has been found regarding the initial introduction of this species, but it is possible that seed was carried in wool, either on sheep or woolen products, yarn, blankets or clothing. *Halogeton glomeratus* (Bieb.) C. A. Mey, another rangeland weed, was introduced via sheep and moved along sheep trails in the western U.S. (Blackwell *et al.* 1979). Squarrose knapweed was among the 526 species introduced in France by seed cleaned out of fleece at a wool yard at Juvénal Gate, where imported wool was washed for 200 years, starting in 1686 (Thellung 1912).

Using the number of seeds produced by the unattacked heads as the potential, overall seed production in squarrose knapweed was reduced by 68 percent. In comparison, seed production in diffuse knapweed was reduced by 95 percent by *Urophora* spp. with no associated change in diffuse knapweed density (Harris 1980b). As a perennial, squarrose knapweed is even less dependent on seedling replacement than the mainly biennial diffuse knapweed to maintain a population. Hence, the greater potential benefit of *Urophora* gall forming flies may be in slowing the rate of spread of squarrose knapweed than in reducing established populations. The individual squarrose head is the unit of dissemination, as compared to the entire plant for diffuse knapweed (Watson and Renney 1974). Because no filled seeds were found in 64% of the heads, the maximum potential success rate of seed dissemination was 36% of the heads.

Reduction in seed number per head to zero is more common in squarrose knapweed than diffuse knapweed because of the relationship of seed number and size to the size of the head. Squarrose and diffuse knapweed heads are similar in size (Wagenitz 1975), but squarrose seeds at 2.778 mg per seed are approximately 2.5 times larger than diffuse seeds at 1.099 mg per seed (Watson and Renney 1974). In the absence of *Urophora* flies, diffuse knapweed averages 12 to 13 seeds per head (Watson and Renney 1974, Harris 1980b, Schirman 1981), while squarrose knapweed heads contain 2 to 3 seeds (Tingey 1960). Thus, physical limitations of space in the squarrose knapweed head and the lower number

of potential seeds both contribute to the effects of the *Urophora* flies. The estimate of a 68 percent reduction in overall seed production may be conservative. Studies of the effect of gall flies on spotted and diffuse knapweed reported that galls act as a metabolic sink, drawing energy from neighboring seed heads (Harris 1980b). Filled seeds are expected to exhibit normal viability. Harris (1980b) reported that although seeds were lighter, germination of plump seeds in spotted and diffuse knapweeds was not affected by gall flies.

Although its presence in California and Utah was documented in the early 1950's, squarrose knapweed should not be discounted as a potentially serious range weed. A period of time between the first occurrence of a weed and its expansion into major infestations over large areas is common. The pattern of spread of an invading species often involves the scattering of satellite populations from an original center of introduction followed by a filling in of intervening areas of suitable habitat (Baker 1972, 1986). No collections of diffuse knapweed were found between the single collection in 1907 (Howell 1959) and the many widely scattered collections in the 1930's (Roché and Talbott 1986). Diffuse knapweed did not become relatively common in eastern Washington until the 1950's nor abundant until the 1970's (Roché and Talbott 1986, Roché 1974). The potential for a similar pattern of expansion exists for squarrose knapweed. It is competitive on rangeland, unpalatable, and tolerant of heavy grazing and other disturbances including plowing and burning (Bellue 1952, Tingey 1960). Containment efforts would be aided by

a more detailed survey of the distribution of squarrose knapweed, particularly the location of satellite populations. The first concern in control of expansion of weed populations is the total area of range occupation and not the density within that area (Moody and Mack 1988).

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